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Seasonal Changes in Chemical Composition and Nutritive Value of Native Forages in a Spruce-Hemlock Forest, Southeastern Alaska

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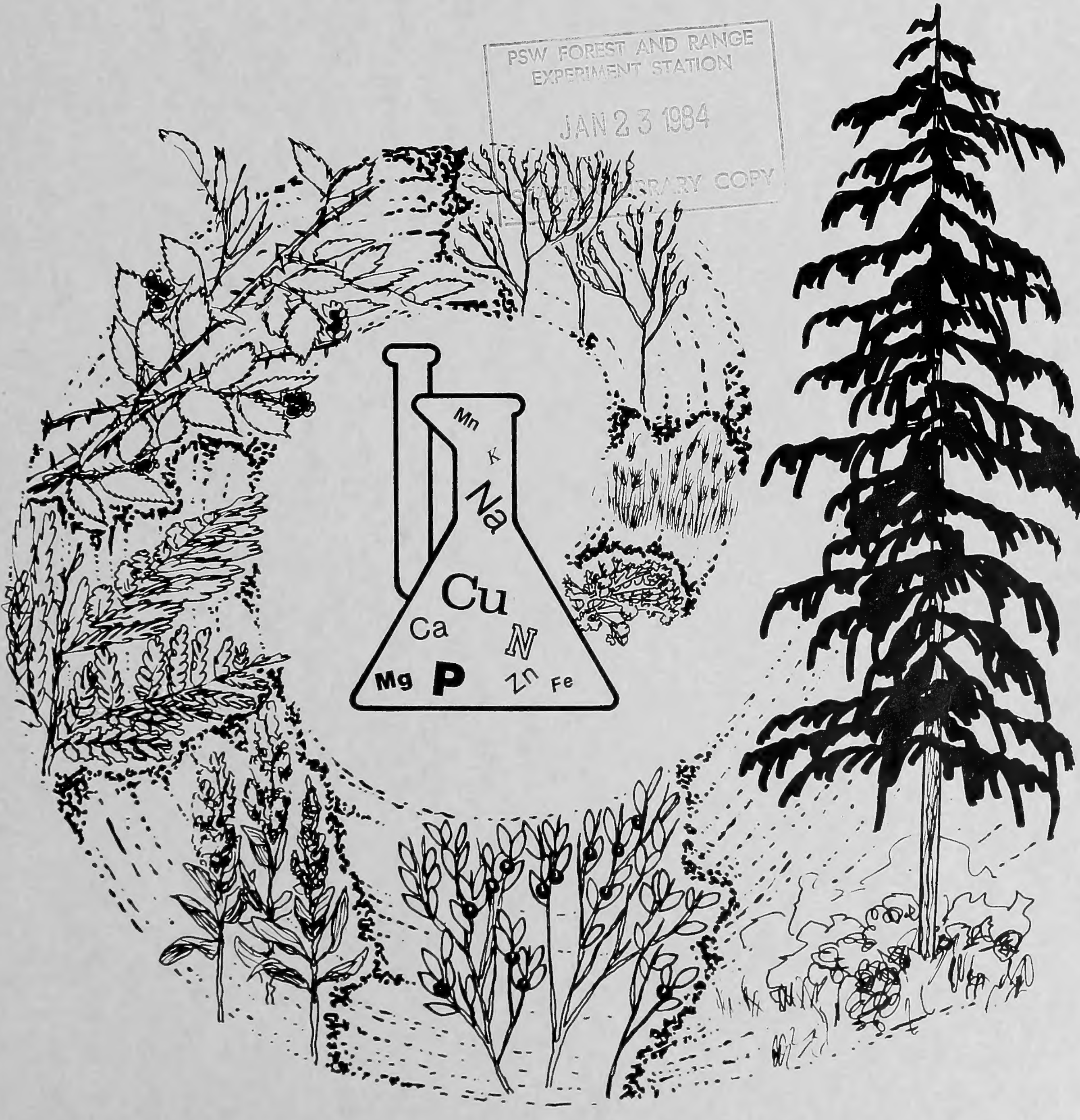

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Abstract

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Twenty-two forages from Admiralty Island, southeastern Alaska, were monitored bimonthly for one year to assess seasonal changes in their chemical composition: neutral detergent fiber, acid detergent fiber, cellulose, lignin/cutin, in-vitro dry-matter digestibility, total nitrogen, phosphorus, potassium, calcium, magnesium, sodium, copper, manganese, iron, and zinc. Seasonal fluctuations were pronounced but generally paralleled the pulse of plant growth in spring-summer. Only minor differences were found in chemical composition of forages from two study areas and results of this study did not differ greatly from results of other studies in southeastern Alaska and the Pacific Northwest. Forbs, half-shrubs, and shrub leaves were consistently the most nutritious forages, especially during winter. Seasonally low levels of digestible energy, nitrogen, and phosphorus were identified as the most important potential limitations of these forages in meeting the nutritional needs of herbivores.

Keywords: Forage production, nutrient analysis, native plants, phytochemistry, phenology, seasonal variations, Alaska (southeastern), southeastern Alaska, wildlife habitat.

Contents

Introduction

The forests of southeastern Alaska provide habitat for a variety of wildlife. As logging and forest management intensify, it becomes increasingly important to understand the relationships between animals and their habitat. Although nutritional relationships provide the biological basis for such an understanding (Moen 1973), little is known about plant-herbivore relationships in southeastern Alaska forests. Livestock grazing has been unimportant in the local economy, so few forage evaluations have been done. The few investigations of forage quality have centered on principal forages utilized by deer (*Odocoileus hemionus sitkensis*) (Klein 1965, Rose 1982, Schoen and Wallmo 1979). Klein (1965) determined the concentrations of nitrogen, fat, fiber, ash, nitrogen free extract, calcium, and phosphorus in 14 species from May through August in central southeastern Alaska. Schoen and Wallmo (1979) measured the nitrogen and fiber content of 10 species during January in northern southeastern Alaska. Rose (1982) measured the nitrogen, phosphorus, total nonstructural carbohydrates, and fiber content of 10 species during January, April, June, and September in southern southeastern Alaska. Data have not been adequate, however, to evaluate seasonal fluctuations in chemical composition and nutritive value across a broad range of forages or to evaluate the role of these fluctuations in limiting the energy, protein, and mineral nutrients available to southeastern Alaska herbivores over an annual cycle.

The objectives of this study were: (1) to obtain a baseline description of the chemical composition of major plant species in southeastern Alaska forests; (2) to quantify seasonal (phenological) changes in chemical composition; (3) to examine site-to-site variability in chemical composition; and (4) to examine the nutritive value of the native forages relative to the dietary requirements of herbivores. The study was intended to provide a basis for modeling nutritional relationships of habitat for herbivores.

Methods

Study Area

Forage species were collected at two sites on Admiralty Island at approximately 58° N latitude, 134° W longitude: Hawk Inlet on the Mansfield Peninsula and Winning Cove on the Glass Peninsula. The sites were 53 km apart (straight line distance). Both were low-elevation forests of uneven-aged, old-growth Sitka spruce (*Picea sitchensis*) [1] and western hemlock (*Tsuga heterophylla*). Dominant understory species included huckleberry (*Vaccinium ovalifolium* and *V. alaskensis*), fool's huckleberry (*Menziesia ferruginea*), devilsclub (*Oplopanax horridum*), and skunk-cabbage (*Lysichiton americanum*), with lesser amounts of bunchberry dogwood (*Cornus canadensis*), trailing bramble (*Rubus pedatus*), foamflower (*Tiarella trifoliata*), and associated plants. Elevation ranged from 0 to 70 m. Climate was cool and wet, typical of the southeastern Alaska coastal rainforest.

Field Collection and Laboratory Analysis of Forage Samples

Samples from 29 species of plants were collected during 1981. Twenty-two species were monitored bimonthly throughout the year at the Hawk Inlet site (table 1), and 17 species were sampled during January and March at the Winning Cove site (table 2). An additional 7 miscellaneous species from other habitats and study sites were sampled for comparative purposes. Samples of vascular species consisted of current annual growth only. Leaves were collected and analyzed separately from stems for tall shrubs (huckleberry, fool's huckleberry, devilsclub, and salmonberry, (*Rubus spectabilis*)). Samples were clipped in the field, refrigerated overnight, oven-dried at 40 °C, ground in a mill with 20-mesh screen, and stored in sealed plastic bags at room temperature (20 °C) until final drying at 50 °C immediately preceding laboratory analyses.

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[1] Nomenclature for vascular plant names follows Hulten (1968) and Hitchcock and Cronquist (1973).

Table 1—Forages collected and dates of collection at the Hawk Inlet study site in 1981

Forage class and species	Jan. 9	Mar. 20	May 27	Aug. 3	Sept. 29	Nov. 30
Forbs and ferns:						
Coptis aspleniifolia	X	X	[1] X	X	X	X
Dryopteris dilatata	X	X	X	X	X	X
Listera cordata			[1] X	[1] X		
Lysichiton americanum		X	X	X	X	
Maianthemum dilatatum			X	X		
Moneses uniflora	X	X	X	X	X	X
Streptopus spp.			[1] X	X		
Tiarella trifoliata	X	X	X	X	X	X
Half-shrubs:						
Cornus canadensis	X	X	X	X	X	X
Rubus pedatus	X	X	X	X	X	X
Vaccinium spp.[2]	X	X	X	X	X	X
Shrubs:						
Menziesia ferruginea—						
Leaves			X	X	X	
Stems	X	X	[3] X	X	X	X
Oplopanax horridum—						
Leaves			X	X	X	
Stems			X	X	X	X
Rubus spectabilis—						
Leaves			X	X	X	
Stems			[1] X	X	X	
Vaccinium alaskensis—						
Leaves			X	X	X	
Stems	X	X	[1] X	X	X	X
Conifers:						
Picea sitchensis	X	X	X	X	X	X
Tsuga heterophylla	X	X	X	X	X	X
Graminoids:						
Deschampsia caespitosa	X		X	X	X	X
Carex lyngbyaei			X	X	X	X

See footnotes at end of table

Table 1—Forages collected and dates of collection at the Hawk Inlet study site in 1981 (continued)

Forage class and species	Jan. 9	Mar. 20	May 27	Aug. 3	Sept. 29	Nov. 30
Lichens:						
Usnea spp.	X	X	X	X	X	X
Moss:						
Rhytidiadelphus loreus	X	X	X	X	X	X
Algae:						
Fucus furcatus	X	X	X	X	X	X

[1] Insufficient material for total ash determination.
[2] Decumbent, evergreen variety.
[3] Insufficient material for detergent analysis, in-vitro dry-matter digestibility, or total ash determination.

Table 2—Forages used in t-test comparisons of Hawk Inlet and Winning Cove study sites

Forage class and species	January 9-15	March 12-20
Forbs and ferns:		
Coptis aspleniifolia	X	X
Dryopteris dilatata		X
Lysichiton americanum		X
Moneses uniflora	X	X
Tiarella trifoliata	X	X
Half-shrubs:		
Cornus canadensis	X	X
Rubus pedatus	X	X
Vaccinium spp.[1]	X	X
Shrubs (stems):		
Alnus rubra		X
Menziesia ferruginea	X	X
Vaccinium alaskensis	X	X
Conifers:		
Picea sitchensis	X	X
Tsuga heterophylla	X	X
Graminoids:		
Elymus arenarius	X	
Lichens:[2]		
Lobaria spp.	X	
Usnea spp.	X	X
Moss:		
Rhytidiadelphus loreus[2]	X	X

[1] Decumbent, evergreen variety.
[2] Lichens and moss were not included in comparisons involving detergent analysis.

Laboratory analyses consisted of sequential detergent analysis (Goering and Van Soest 1970) as modified by Mould and Robbins (1982) for fiber constituents and Tilley and Terry in-vitro digestion trials (Goering and Van Soest 1970) of 12- and 48-h duration using cattle rumen fluid. Nutrient contents were determined in the following manner: Aliquots of pulverized and dried tissue were weighed into glass digestion tubes and digested for 1 h in a 40-unit aluminum block at 400 °C. The digestion mixture consisted of 7 ml H_2SO_4-H_2SeO_3 and 3 ml 30-percent H_2O_2 per aliquot. The acid component was prepared by dissolving 97 g H_2SeO_3 in 100 ml deionized water. That solution was then mixed with 2 350 ml concentrated H_2SO_4. After digestion, samples were cooled and each was brought to 75-ml volume with deionized water. An aliquot from each digest was sealed in polyethylene sample vials. Nitrogen (N) and phosphorus (P) were measured simultaneously on a Technicon Auto Analyzer II [2]/. Potassium (K), magnesium (Mg), sodium (Na), iron (Fe), copper (Cu), zinc (Zn), and manganese (Mn) were measured on a Perkin-Elmer 5000. All analyses were compared with National Bureau of Standards' orchard leaf reference sample. Analytical accuracy was monitored by including one known composition tissue in each lot of 40 samples analyzed. All analyses were expressed on a dry-weight (at 50 °C) basis.

Data Analysis

Data for the samples from the Hawk Inlet study site are reported in the appendix to provide a baseline description of the chemical composition of major plant species. Annual means were calculated for all species. To analyze seasonal changes in chemical composition, we calculated means for each forage class (forbs and ferns, half-shrubs, shrubs, graminoids, etc.) for each collection date. In calculating means for shrubs, we weighted leaf and stem values in proportion to the leaf:stem ratio of 150 ovendry huckleberry twigs clipped at the collection site at the time of each collection.

As an index of the amount of digestion-inhibiting secondary plant compounds, we calculated the difference between the amount of dry matter that disappeared in 48-h in-vitro tests and the digestibility predicted by the equation of Mould and Robbins (1982), which is based on the fiber composition of forage. The Mould-Robbins equation is based on forages that were relatively free of digestion-inhibiting secondary compounds. We believe that values of in-vitro dry-matter disappearance that were exceptionally lower than predicted by the Mould-Robbins equation indicate a high content of digestion inhibitors.

Variability in chemical composition of forages from site to site was examined across species by comparing means of samples collected from the Hawk Inlet and Winning Cove study sites in January and March. Any biases stemming from differential phenology at the two study sites were minimized, because plants were relatively dormant at those times. Means for both collection dates and each chemical variable of samples from the two sites were compared and tested for statistical significance with a paired-sample t-test, pairing by species (table 2), with $P \leq 0.05$ considered as statistically significant.

Nutritive value of the forages was evaluated by comparing chemical composition and digestibility with standards of the National Research Council (1976) for nutritional requirements of beef cattle. These requirements are well known and are used here only as an index of the nutritional value of southeastern Alaska forages for herbivores and to identify major potential nutritional limitations.

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[2] Use of brand names does not imply endorsement by either the U.S. Department of Agriculture or the University of Alaska.

Results and Discussion

Fiber Constituents

Neutral detergent fiber (NDF), which consists mainly of the total cell wall fraction of the forage, was greatest in moss, graminoids, and shrub stems, and least in lichens, algae, forbs, and shrub leaves (table 3). Neutral detergent solubles (NDS), mainly the cell cytoplasm and its constituents, were especially great in skunk-cabbage, heartleaf twayblade (*Listera cordata*), and deerberry (*Maianthemum dilatatum*). Lignin-cutin content, a component of NDF, was relatively great in moss, conifers, shrub stems, and spreading woodfern (*Dryopteris dilatata*). While NDS tends to be rapidly and completely digested by ruminants, lignin-cutin is virtually nondigestible and retards cellulose digestion (Goering and Van Soest 1970).

Forbs, ferns, and half-shrubs had the greatest NDS content throughout the year (fig. 1). Conifers and shrubs, on the other hand, were consistently high in lignin/cutin (fig. 2). The fiber content and composition of conifers, forbs, and half-shrubs remained relatively stable throughout the year, whereas in shrubs, it exhibited pronounced seasonal fluctuations corresponding with the production and loss of leaves.

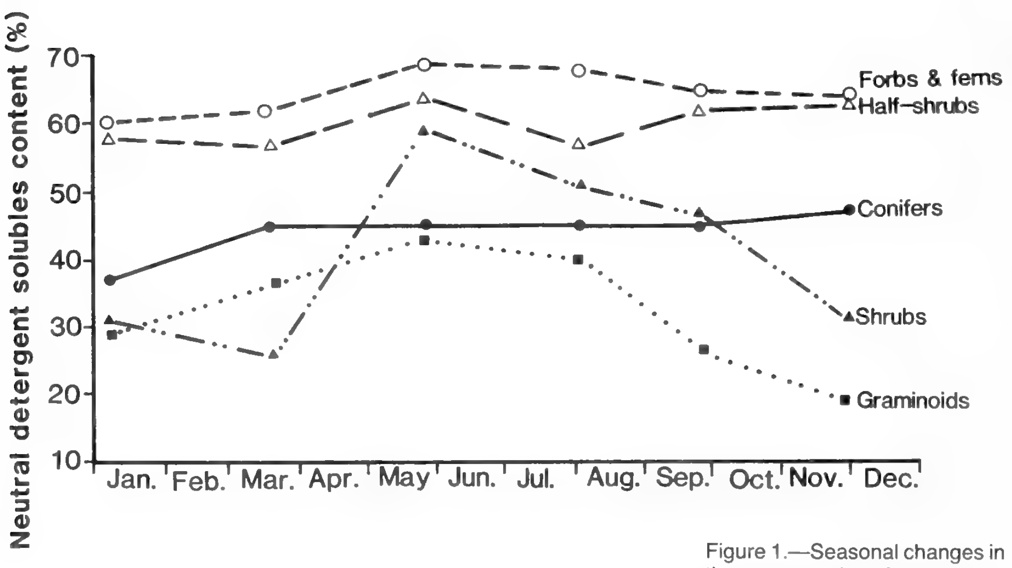

Figure 1.—Seasonal changes in the concentration of neutral detergent solubles.

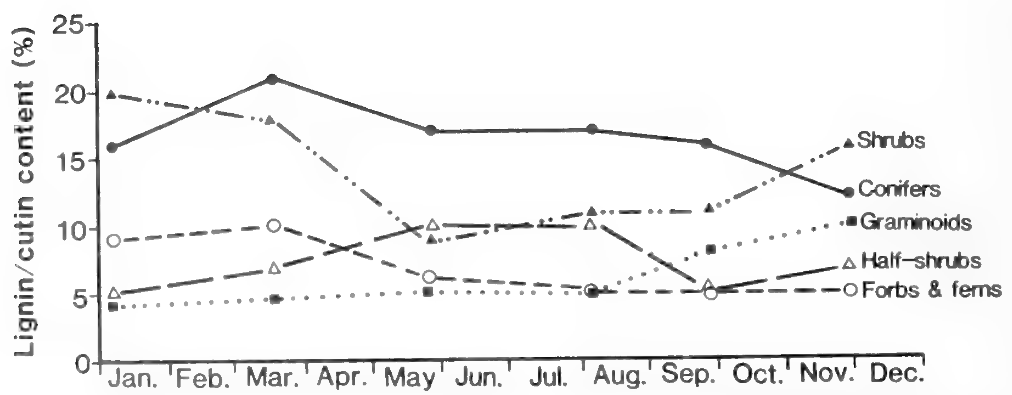

Figure 2.—Seasonal changes in the concentration of lignin/cutin.

Table 3—Mean values of variables measured in detergent analysis for each species

Forage class and species	NDF	ADF	Cellulose	Lignin/cutin
	Percent dry weight			
Forbs and ferns:				
Coptis aspleniifolia	43.8	28.7	24.1	4.2
Dryopteris dilatata	49.7	36.2	20.4	15.4
Listera cordata	23.9	16.6	13.4	3.2
Lysichiton americanum	20.8	13.6	10.4	2.0
Maianthemum dilatatum	25.3	16.4	14.1	1.5
Moneses uniflora	28.6	17.4	13.2	4.4
Streptopus spp.	27.3	19.3	17.1	0.9
Tiarella trifoliata	34.4	25.3	15.2	9.7
Half-shrubs:				
Cornus canadensis	32.3	21.5	14.8	6.1
Rubus pedatus	34.2	17.4	14.1	2.8
Vaccinium spp.[1]	53.3	35.4	22.4	12.8
Shrubs:				
Menziesia ferruginea—				
Leaves	38.2	23.0	15.0	7.8
Stems	74.8	56.1	31.6	18.2
Oplopanax horridum—				
Leaves	31.0	16.7	11.8	4.5
Stems	56.8	41.6	29.5	11.5
Rubus spectabilis—				
Leaves	30.4	14.0	9.0	5.1
Stems	66.2	42.3	29.8	12.4
Vaccinium alaskensis—				
Leaves	53.3	30.6	15.4	15.2
Stems	66.6	49.2	29.1	18.1
Conifers:				
Picea sitchensis	59.5	44.4	26.7	17.4
Tsuga heterophylla	52.4	38.7	22.4	15.1
Graminoids:				
Deschampsia caespitosa	69.1	36.4	27.5	6.2
Carex lyngbyaei	67.6	34.8	27.1	7.2
Lichens:				
Usnea spp.	27.5	4.5	[2]1.6	[2]2.2
Moss:				
Rhytidiadelphus loreus	81.8	51.6	30.8	20.1
Algae:				
Fucus furcatus	27.8	19.5	6.8	11.9

[1] Decumbent, evergreen variety.

[2] Lichens differ chemically from vascular plants; values reported are not really cellulose or lignin/cutin.

Dry Matter Digestibility

Differences in fiber composition among species were largely reflected in differences in in-vitro dry-matter digestibility (IVDMD) (table 4). Species high in NDS and low in lignin/cutin content tended to be digested most completely and rapidly (for example, skunk-cabbage, heartleaf twayblade, deerberry, and devilsclub leaves). The 48-h IVDMD values of several species, however, were much lower than would be expected on the basis of their fiber composition: twistedstalk (*Streptopus* spp.), trailing bramble, fool's huckleberry, salmonberry, Sitka spruce, western hemlock, hairgrass (*Deschampsia cespitosa*), sedge (*Carex lyngbyaei*), beard lichen (*Usnea* spp.), feathermoss (*Rhytidiadelphus loreus*), and rockweed alga (*Fucus furcatus*). Because both the detergent analysis and the Mould-Robbins equation were developed for vascular forages, particularly grasses and forbs, there are inherent problems in applying the technique and equation to lichens, moss, and algae. Conifers are known to contain high levels of digestion-inhibiting volatile oils (Oh and others 1967). The graminoids in this study contained an appreciable amount of silica during winter (mean ± standard deviation: 2.7 ± 3.2 percent for 8 random samples of graminoids taken in September through January, compared with 0.1 ± 0.1 percent for 4 random samples of graminoids taken in May through August, and 0.0 ± 0.0 percent for 15 random samples of dicots collected the year around).[3] Silica is known to inhibit the digestibility of dry matter (Van Soest and Jones 1968). The fact that IVDMD of the other species was lower than expected, however, indicates a relatively high content of digestion-inhibiting substances in them as well.

Forbs were highly digestible throughout the year (fig. 3). Half-shrubs also were highly digestible but apparently were more digestible in winter than in summer. Conifers were poorly digestible the year around, while IVDMD of shrubs paralleled changes in the production and loss of leaf tissue. Graminoids were relatively highly digestible in spring and early summer but poorly digestible in late fall and winter. Forbs and half-shrubs were the forages most rapidly digestible (fig. 4) in both summer and winter. Shrubs and graminoids were more rapidly digestible than conifers in summer but less rapidly digestible than conifers in winter. Effects of digestion inhibitors were most apparent in conifers, shrubs, and graminoids during winter (fig. 5).

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[3]Hanley, Thomas A. and McKendrick, J. D. Unpublished data on file at Forestry Sciences Laboratory, Juneau.

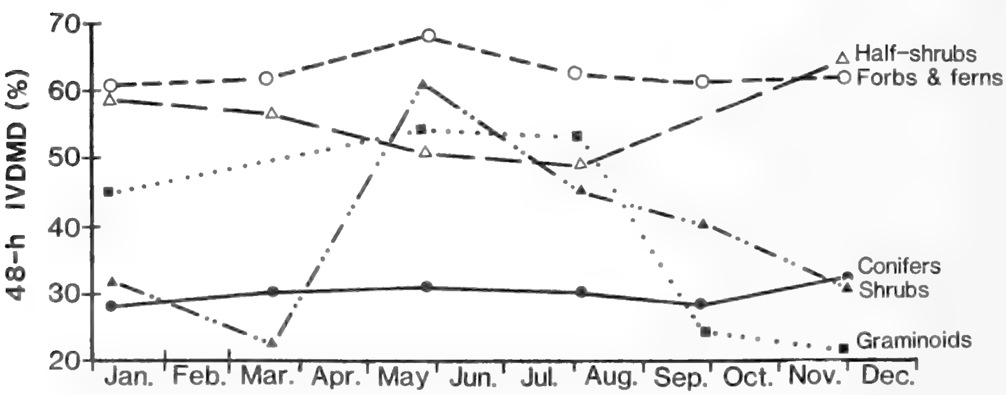

Figure 3.—Seasonal changes in 48-h in-vitro dry-matter digestibility (IVDMD).

Table 4—Mean values of in-vitro dry-matter digestibility trials for each species and percentage difference between observed (48-h) and predicted digestibility

Forage class and species	Digestibility 12 h	48 h	Difference between observed and expected [1]
	Percent dry weight		
Forbs and ferns:			
Coptis aspleniifolia	46.7	67.0	-2.6
Dryopteris dilatata	34.1	43.4	-9.1
Listera cordata	61.2	76.0	-5.3
Lysichiton americanum	63.5	78.0	-0.2
Maianthemum dilatatum	63.7	71.5	-12.4
Moneses uniflora	54.0	68.3	-6.0
Streptopus spp.	55.9	70.0	-21.1
Tiarella trifoliata	43.2	54.5	-8.8
Half-shrubs:			
Cornus canadensis	47.1	65.9	-5.2
Rubus pedatus	40.5	50.9	-30.0
Vaccinium spp.[2]	38.7	50.5	+8.1
Shrubs:			
Menziesia ferruginea—			
Leaves	39.9	50.3	-15.4
Stems	18.4	24.0	-36.3
Oplopanax horridum—			
Leaves	60.0	73.3	+10.0
Stems	43.3	53.7	+4.4
Rubus spectabilis—			
Leaves	45.2	46.1	-29.5
Stems	25.4	33.7	-21.5
Vaccinium alaskensis—			
Leaves	40.7	46.7	+15.2
Stems	27.6	34.1	-6.6
Conifers:			
Picea sitchensis	27.7	28.9	-28.0
Tsuga heterophylla	29.6	30.5	-34.3

See footnotes at end of table

Table 4—Mean values of in-vitro dry-matter digestibility trials for each species and percentage difference between observed (48-h) and predicted digestibility (continued)

Forage class and species	Digestibility 12 h	48 h	Difference between observed and expected [1]
	---------------- Percent dry weight ----------------		
Graminoids:			
Deschampsia caespitosa	29.7	37.9	-33.6
Carex lyngbyaei	31.0	39.4	-24.1
Lichens:			
Usnea spp.	18.8	21.5	-65.5
Moss:			
Rhytidiadelphus loreus	15.5	16.0	-29.5
Algae:			
Fucus furcatus	45.5	36.3	-39.7

[1] Percentage difference is [(Observed – Expected)/(Expected)] x 100, where Expected is the value predicted using the summative equation of Mould and Robbins (1982) for in-vitro apparent dry-matter digestibility of forages in which soluble phenolics and other digestion-inhibiting compounds are minimal. The equation of Mould and Robbins (1982) was for white-tailed deer (*Odocoileus virginianus*).

[2] Decumbent, evergreen variety.

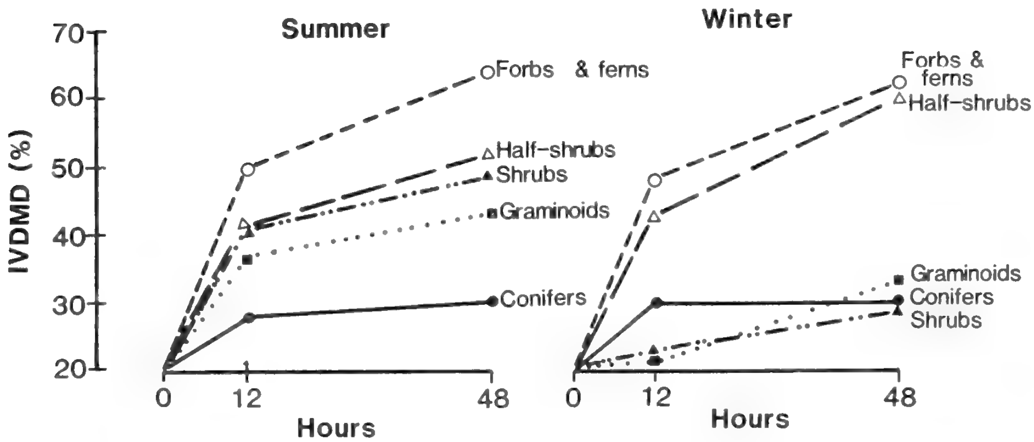

Figure 4.—Summer and winter values of 12- and 48-h in-vitro dry-matter digestibility (IDVMD) trials.

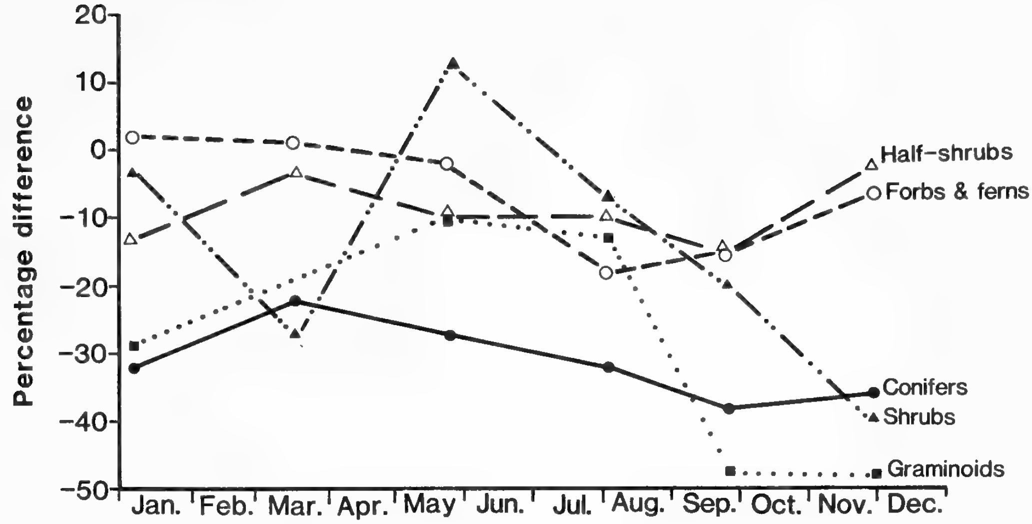

Figure 5.—Seasonal changes in percentage difference between observed and predicted digestibility (see table 4).

Macronutrients

Total ash concentration of the forages did not vary much seasonally, except in graminoids, which were collected along the beach-forest fringe and were exposed to periodic inundation by salt water (fig. 6). Forbs and half-shrubs were consistently highest in total ash concentration, while conifers and shrub stems were consistently low.

N concentration was greatest in forbs, ferns, half-shrubs, and shrub leaves (especially skunk-cabbage, twisted-stalk, and devilsclub leaves), and lowest in beard lichen and feathermoss (table 5). N concentration was consistently low in conifers but increased with summer growth in the other vascular species (fig. 7). P concentration exhibited a pattern nearly identical to that of N (table 5, fig. 8).

Forbs and ferns consistently contained the greatest amounts of K (table 5, fig. 9). Devilsclub leaves and stems and rockweed alga also were high in K. Lowest levels consistently occurred in beard lichen, feathermoss, and conifers. Graminoids and shrub stems were very low in K during winter and highest during the pulse of growth in spring and early summer.

Ca concentrations were generally about 3 to 4 times greater than P concentrations (table 5). In contrast to P, however, Ca was lowest during the pulse of growth in spring and early summer (fig. 10). Ca to P ratios were nearly balanced in shrubs and forbs in early summer but very unbalanced throughout the rest of the year. Ca concentration was consistently greatest in bunchberry dogwood and foamflower and consistently low in conifers, graminoids, beard lichen, feathermoss, and fool's huckleberry stems.

Throughout the year, herbaceous forage contained the greatest concentration of Mg (fig. 11). Beard lichen, feathermoss, conifers, and shrub stems contained the lowest levels. Na concentration was consistently low in conifers and half-shrubs, and was consistently greatest in rockweed alga, graminoids, and forbs (especially skunk-cabbage) (table 5, fig. 12). Shrubs were relatively high in Na during late summer and fall. Wide fluctuations in the Na concentration of graminoids probably reflected periodic inundation by salt water.

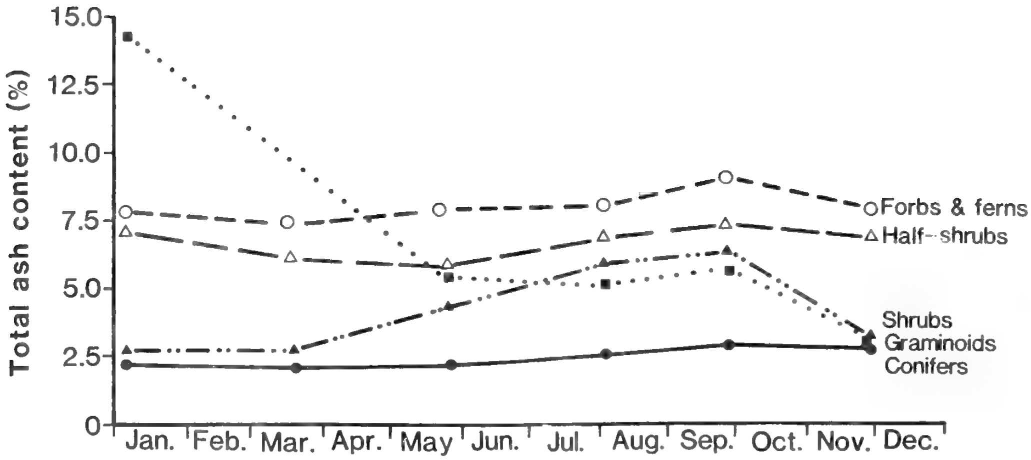

Figure 6.—Seasonal changes in the concentration of total ash.

Table 5—Mean values of percentage composition of macronutrients for each species

Forage class and species	N	P	K	Ca	Mg	Na
	Percent dry weight					
Forbs and ferns:						
Coptis aspleniifolia	1.81	0.22	1.65	0.79	0.31	0.06
Dryopteris dilatata	2.21	0.28	2.43	0.60	0.41	0.14
Listera cordata	2.51	0.42	3.99	0.63	0.21	0.27
Lysichiton americanum	5.63	0.52	2.49	1.33	0.23	1.01
Maianthemum dilatatum	2.03	0.30	2.40	0.50	0.22	0.66
Moneses uniflora	2.01	0.27	1.80	0.66	0.23	0.13
Streptopus spp.	3.48	0.38	4.32	1.15	0.33	0.06
Tiarella trifoliata	2.04	0.25	2.52	1.95	0.40	0.19
Half-shrubs:						
Cornus canadensis	2.01	0.22	1.04	2.58	0.49	0.05
Rubus pedatus	2.03	0.24	1.37	0.72	0.48	0.07
Vaccinium spp.[1]	1.52	0.16	0.75	0.85	0.20	0.09
Shrubs:						
Menziesia ferruginea—						
Leaves	2.48	0.24	1.19	0.62	0.40	0.47
Stems	1.18	0.15	0.85	0.35	0.17	0.09
Oplopanax horridum—						
Leaves	3.31	0.43	2.43	1.29	0.19	0.51
Stems	2.02	0.34	2.22	0.88	0.18	0.27
Rubus spectabilis—						
Leaves	2.25	0.35	1.30	0.89	0.40	0.21
Stems	0.96	0.20	1.30	0.46	0.17	0.17
Vaccinium alaskensis—						
Leaves	2.79	0.20	1.08	1.22	0.39	0.30
Stems	1.42	0.18	0.73	0.65	0.16	0.07

See footnote at end of table

Table 5—Mean values of percentage composition of macronutrients for each species (continued)

Forage class and species	N	P	K	Ca	Mg	Na
			Percent dry weight			
Conifers:						
Picea sitchensis	1.05	0.19	0.66	0.36	0.08	0.07
Tsuga heterophylla	1.01	0.19	0.51	0.34	0.10	0.08
Graminoids:						
Deschampsia caespitosa	1.43	0.14	1.06	0.21	0.17	0.68
Carex lyngbyaei	1.16	0.17	1.35	0.36	0.14	0.36
Lichens:						
Usnea spp.	0.44	0.10	0.22	0.29	0.06	0.07
Moss:						
Rhytidiadelphus loreus	0.62	0.13	0.43	0.30	0.09	0.07
Algae:						
Fucus furcatus	1.41	0.17	2.68	1.06	0.72	2.83

[1] Decumbent, evergreen variety.

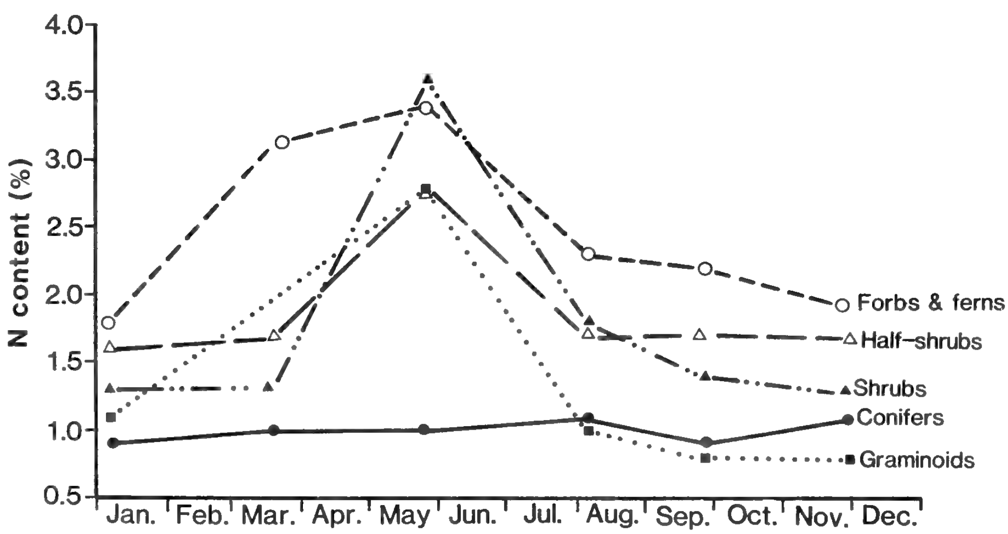

Figure 7.—Seasonal changes in the concentration of total nitrogen.

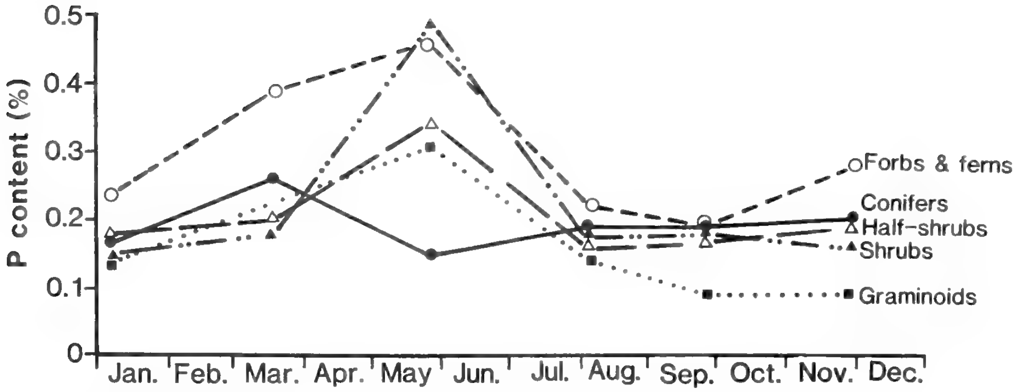

Figure 8.—Seasonal changes in the concentration of phosphorus.

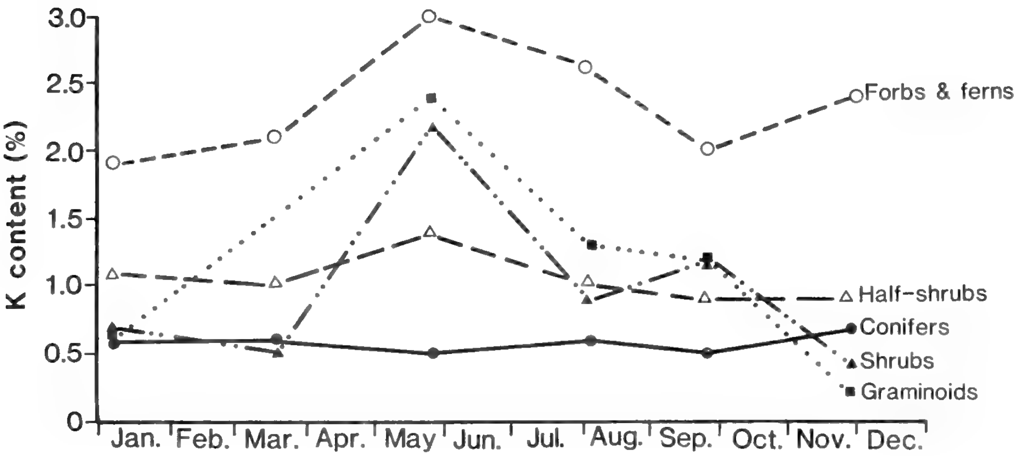

Figure 9.—Seasonal changes in the concentration of potassium.

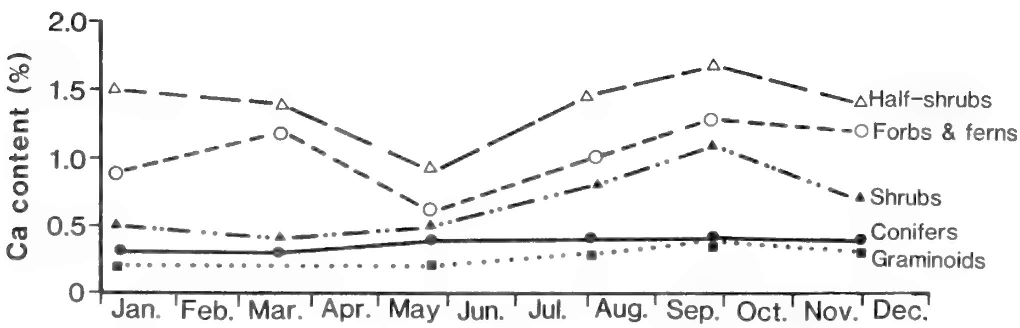

Figure 10.—Seasonal changes in the concentration of calcium.

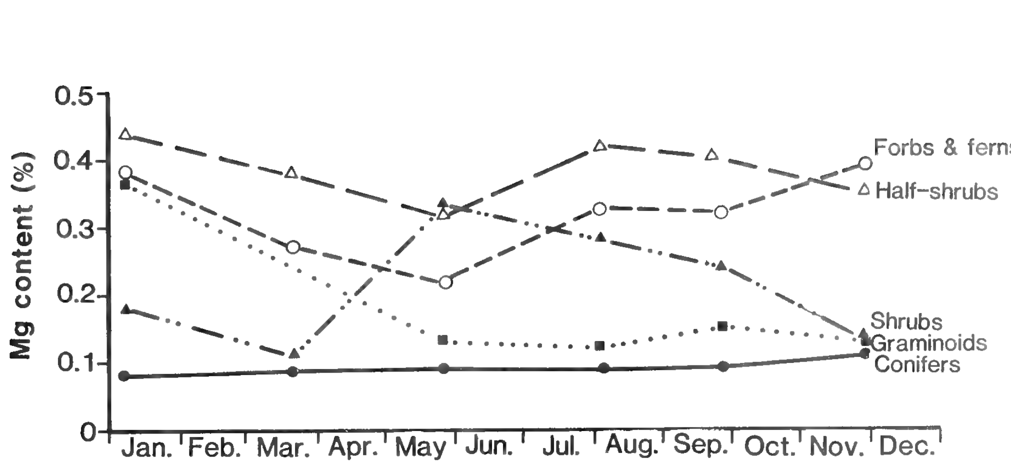

Figure 11.—Seasonal changes in the concentration of magnesium.

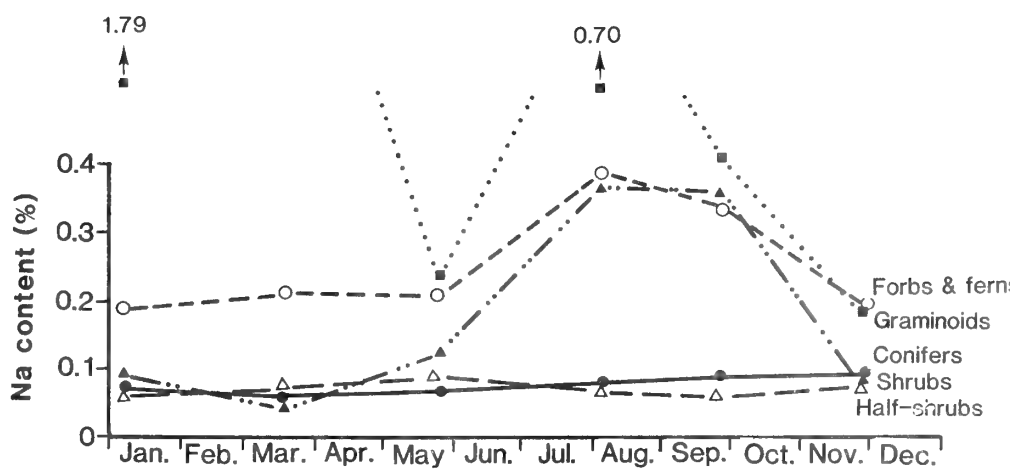

Figure 12.—Seasonal changes in the concentration of sodium.

Micronutrients

Shrubs and forbs (especially skunk-cabbage, heartleaf twayblade, and twisted-stalk) contained the greatest amounts of Cu throughout the year (table 6, fig. 13). Greatest concentrations occurred in spring and early summer. Concentrations in conifers, beard lichen, and rockweed alga were consistently low, and very low in graminoids in late fall and winter.

Very high concentrations of Mn were observed in many forages: skunk-cabbage, trailing bramble, huckleberry, fool's huckleberry, Sitka spruce, western hemlock, and feathermoss all averaged more than 1,000 ppm (table 6) and were consistently high (fig. 14). Graminoids, forbs, bunchberry dogwood, devilsclub, salmonberry, beard lichen, and rockweed alga contained moderate to low levels.

Table 6—Mean values of micronutrient composition for plant species

Forage class and species	Cu	Mn	Fe	Zn
	Parts per million dry weight			
Forbs and ferns:				
Coptis aspleniifolia	5.3	326.0	62.7	177.6
Dryopteris dilatata	9.2	668.1	105.7	44.2
Listera cordata	11.0	913.0	84.5	68.6
Lysichiton americanum	13.8	1794.8	101.8	43.4
Maianthemum dilatatum	3.0	523.9	39.5	23.6
Moneses uniflora	8.2	609.8	169.0	34.9
Streptopus spp.	10.0	296.1	68.0	52.4
Tiarella trifoliata	6.5	321.9	237.8	46.7
Half-shrubs:				
Cornus canadensis	5.2	211.6	75.3	86.6
Rubus pedatus	7.2	1237.6	98.8	31.9
Vaccinium spp.[1]	7.0	3117.3	57.5	33.4
Shrubs:				
Menziesia ferruginea—				
Leaves	10.0	16656.7	62.0	86.6
Stems	11.8	7139.2	22.8	40.5
Oplopanax horridum—				
Leaves	16.0	242.4	64.0	42.6
Stems	11.8	84.4	38.3	65.4
Rubus spectabilis—				
Leaves	5.0	84.8	58.7	82.0
Stems	18.3	36.9	19.3	116.4
Vaccinium alaskensis—				
Leaves	11.3	1961.3	51.3	18.6
Stems	12.0	2021.6	23.2	39.5
Conifers:				
Picea sitchensis	3.2	1299.3	23.3	27.8
Tsuga heterophylla	3.3	1947.2	66.2	14.2
Graminoids:				
Deschampsia caespitosa	4.0	201.1	254.2	20.6
Carex lyngbyaei	2.8	695.6	102.0	22.6
Lichens:				
Usnea spp.	1.7	220.9	56.7	28.6
Moss:				
Rhytidiadelphus loreus	5.2	1050.8	348.3	23.8
Algae:				
Fucus furcatus	1.8	43.5	158.2	22.2

[1] Decumbent, evergreen variety.

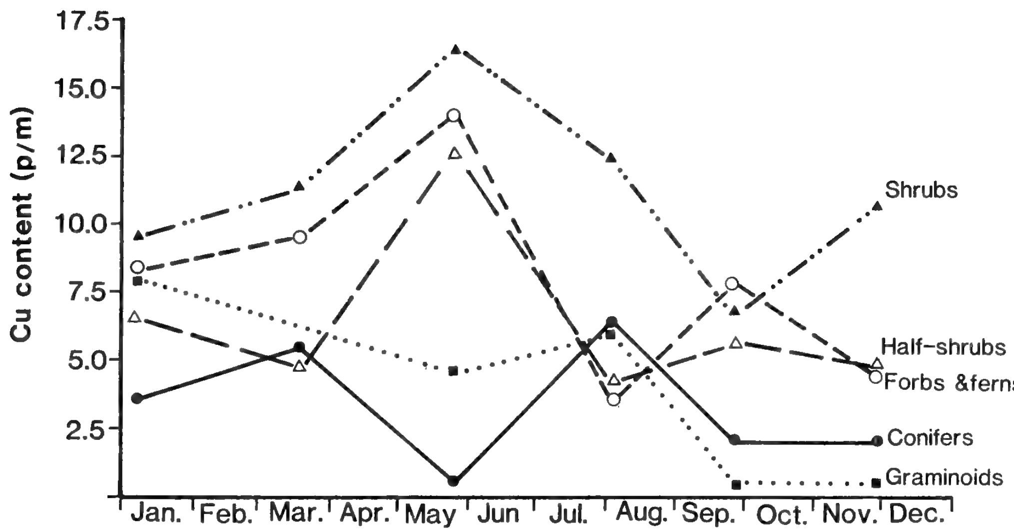

Figure 13.—Seasonal changes in the concentration of copper.

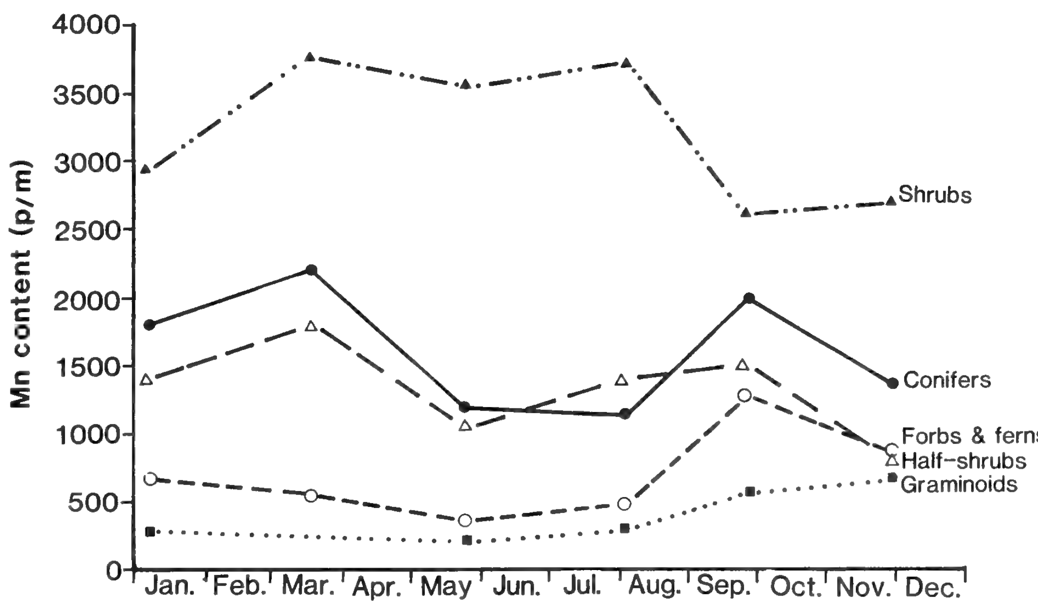

Figure 14.—Seasonal changes in the concentration of manganese.

Fe concentrations were greatest in forbs, ferns, feathermoss, and rockweed alga throughout the year (table 6, fig. 15). High concentrations in graminoids (especially hairgrass) corresponded with peak concentrations of total ash and Na and probably reflected recent inundation by salt water. Shrubs, conifers, and beard lichen were consistently low in Fe.

Zn values were greatest in fernleaf goldthread (*Coptis aspleniifolia*), bunchberry dogwood, and salmonberry (table 6). They were relatively stable throughout the year in half-shrubs, graminoids, and conifers (fig. 16).

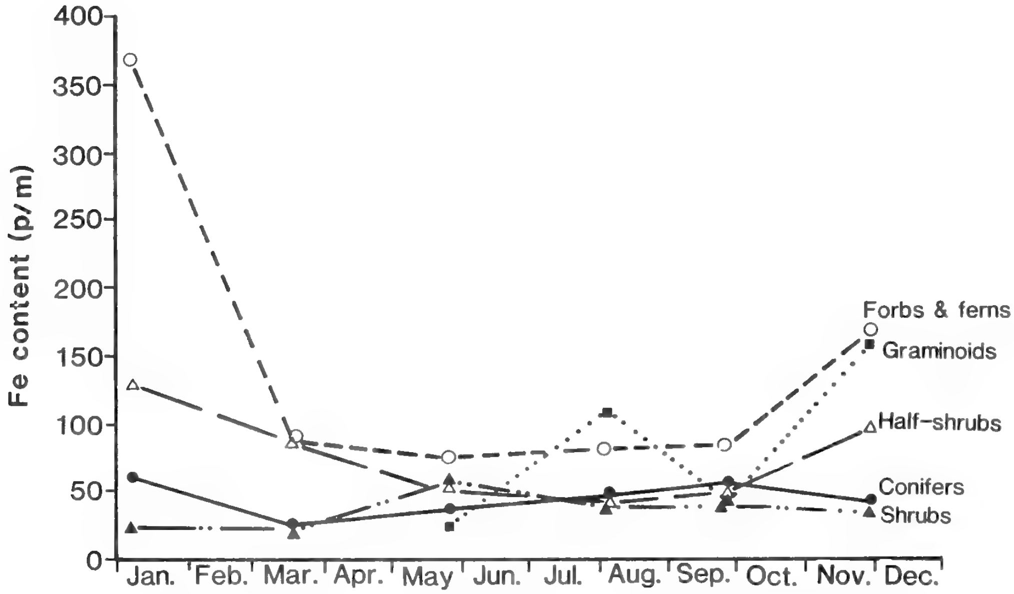

Figure 15.—Seasonal changes in the concentration of iron.

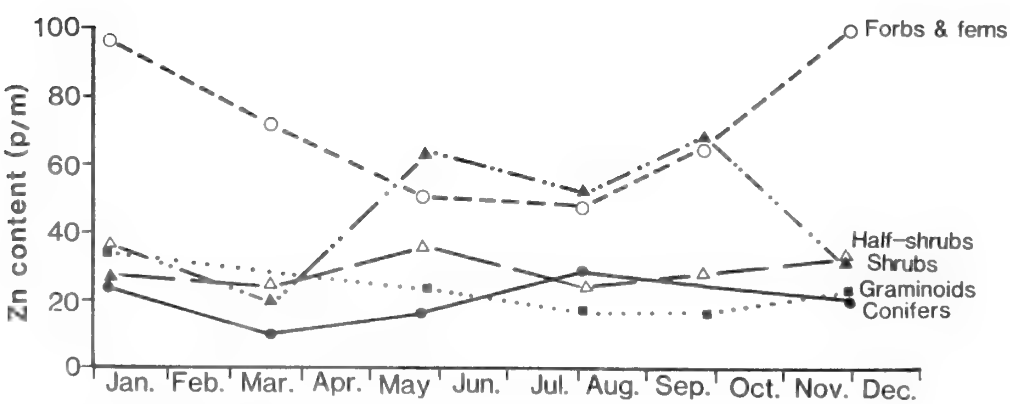

Figure 16.—Seasonal changes in the concentration of zinc.

Miscellaneous Species from Other Habitats

The seven miscellaneous forages we analyzed came from a variety of habitats. Each differed from samples of its respective forage class from Hawk Inlet in one or more nutritional variables (table 7). The subalpine forb, deer-cabbage (*Fauria crista-galli*) was especially high in IVDMD, Na, Cu, and Zn, and low in K and Ca. Crowberry (*Empetrum nigrum*), a half-shrub from muskeg, was high in lignin/cutin and Cu, and low in IVDMD, N, P, K, Ca, and Mg. Red alder (*Alnus rubra*) stems were low in NDF (high in NDS) and Mn. Labrador-tea (*Ledum palustre*), a shrub from muskeg, was low in NDF and Cu, and high in IVDMD and Fe. Alaska yellow cedar (*Chamaecyparis nootkatensis*) was high in IVDMD, total ash, Ca, and Zn, and low in NDF, P, and Mn. Lyme grass (*Elymus arenarius*) was very high in Fe, but it, like the other graminoids, was subject to periodic inundation by salt water. The foliose lichen *Lobaria* differed from beard lichen, being higher in NDF, "lignin/cutin," N, K, Mn, and Fe. All forages from miscellaneous sources except deer-cabbage had 48-h IVDMD values much lower than expected on the basis of the Mould-Robbins equation for fiber constituents. Deer-cabbage appeared relatively free of digestion-inhibiting secondary compounds.

Table 7—Chemical composition and dry-matter digestibility of 7 miscellaneous forages collected in various habitats in 1981

	Fauria Crista-galli, subalpine, 8/17	*Empetrum nigrum*, muskeg, 3/26	*Alnus rubra* stems, beach, 3/20	*Ledum palustre*, [1] muskeg, 3/26	*Chamaecyparis nootkatensis* forest, 2/25	*Elymus arenarius* beach, 1/9	*Lobaria* spp. forest, 1/9
	Percent						
NDF	28.3	53.4	51.8	49.9	39.7	77.3	61.0
ADF	12.4	39.6	39.4	49.9	31.1	39.6	29.3
Cellulose	10.6	17.4	18.2	19.2	22.6	23.7	15.8
Lignin-Cutin	1.7	22.2	21.1	15.6	8.6	5.1	9.8
12-h IVDMD	69.7	22.5	31.1	29.6	38.7	20.5	28.0
48-h IVDMD	78.6	29.9	34.2	39.9	47.3	31.0	29.2
Observed-Expected DMD	+3.1	-21.5	-15.4	-12.2	-22.8	-46.3	-31.5
Total Ash	8.5	[2]	2.0	1.7	5.4	17.2	2.3
N	2.61	0.90	1.77	1.09	1.00	0.92	3.57
P	0.26	0.08	0.15	0.10	0.12	0.11	0.19
K	1.07	0.22	0.40	0.28	0.44	0.42	0.63
Ca	0.57	0.45	0.31	0.39	1.74	0.18	0.15
Mg	0.36	0.10	0.12	0.09	0.11	0.37	0.07
Na	1.48	0.03	0.09	0.04	0.04	0.81	0.10
	Parts per million						
Cu	15.0	9.0	9.0	6.0	3.0	5.0	4.0
Mn	740.0	314.2	69.2	747.6	73.9	370.2	1180.4
Fe	67.0	56.0	44.0	258.0	35.0	4000.0	160.0
Zn	225.1	21.8	30.5	60.7	163.4	34.6	34.1

[1] Includes both stems and leaves.

[2] Insufficient amount of sample for ash determination.

Comparisons Between Study Areas

Of 36 comparisons of means between the Hawk Inlet and Winning Cove study areas, only 3 were statistically different (table 8). In January, Hawk Inlet forages were lower in P and higher in Cu than the Winning Cove forages; there were no differences, however, in March. Similarly, although Hawk Inlet forages were lower in Mg concentration than Winning Cove forages in March, there was no such difference in January. Generally, there appeared to be no biologically significant differences in forages from the two study areas.

The Hawk Inlet forages differed slightly from those reported by other investigators in southeastern Alaska and the Pacific Northwest (table 9). No clear geographic pattern is evident, however, and the results were generally very similar. For example, the very high N values reported in this study for skunk-cabbage are similar to those reported by both Klein (1965) and Rose (1982). Klein also observed a Ca to P ratio greater than unity (about 2:1) on all four of his study areas. There was, however, a major discrepancy between our results for beard lichen and those reported by others. Mean annual 48-h IVDMD for beard lichen from Hawk Inlet was 21.5 percent. In contrast, Rochelle (1980) reported a mean annual value of 72.5 percent for *Alectoria sarmentosa,* a different beard lichen but similar to *Usnea* spp. in appearance, N concentration, and fiber composition. *Alectoria sarmentosa* collected in November at Hawk Inlet had a 48-h IVDMD of 26.3 percent, in comparison to 23.9 percent for *Usnea* spp. collected at the same time and place. The difference between Rochelle's results and ours probably reflects the difference in source of rumen inoculum. Rochelle used deer rumen fluid; we used cattle rumen fluid. The difference for most species is minor; for example, Rochelle's results and ours differed little for huckleberry and western hemlock (table 9). The chemical structure of lichens differs from that of vascular forages, however, and our cattle rumen fluid probably contained few microbes adapted for lichen digestion. Rochelle's IVDMD values for lichens are probably more appropriate than ours for deer on diets containing lichens.

Nutritive Value

The nutrient requirements of beef cattle (table 10) provide one standard for evaluating the nutritive value of the Hawk Inlet forages. Assuming a gross energy content of 4.4 kcal g^{-1} and a direct, linear relationship between digestible dry matter and digestible energy (Rittenhouse and others 1971, Mautz and others 1974), it is apparent that digestible dry matter must be at least 43 to 52 percent to meet maintenance requirements during winter and 43 to 70 percent to meet maintenance, growth, and lactation requirements during summer. Of the Hawk Inlet forages, forbs and half-shrubs satisfy the winter requirement, while forbs, half-shrubs, shrub leaves, and graminoids satisfy the summer requirement. The digestible energy content of conifers and shrub stems is inadequate throughout the year for maintenance requirements. Moss and algae also are inadequate. Lichens, however, constitute a high-energy food source (Rochelle 1980). During winter, when the availability of forbs and half-shrubs is reduced by snow, lichens are probably very important sources of energy for wild ruminants. Energy deficits during winter can be offset partially by accumulated fat. The potential limiting role of energy is not a simple, straightforward matter, however, because energy requirements vary with activity and energy intake varies with diet choice.

Requirements for crude protein (N x 6.25) indicate that a minimum N concentration of 0.94 to 1.41 percent is required for maintenance alone, 1.36 to 1.53 percent for maintenance and growth, and 1.47 to 1.74 percent for maintenance and lactation. Forbs and ferns, half-shrubs, and shrubs satisfy these requirements year around, and graminoids satisfy them in early summer. Conifers, feathermoss and beard lichen are inadequate the year around. The foliose lichen *Lobaria,* however, with an N concentration of 3.57 percent, exceeded even the lactation requirements. Rockweed alga could satisfy requirements for maintenance and some growth but not for reproduction.

Table 8—Comparison of mean values of variables measured for Hawk Inlet and Winning Cove study sites

Variable	Hawk Inlet		Winning Cove		Significance [1]	
	Jan.	Mar.	Jan.	Mar.	Jan.	Mar.
	Percent					
NDF	52.5	48.6	51.7	48.0	NS	NS
ADF	36.0	33.6	35.6	32.5	NS	NS
Cellulose	24.4	16.4	22.5	17.9	NS	NS
Lignin-cutin	9.9	13.1	11.5	11.0	NS	NS
12-h IVDMD	32.4	36.0	33.4	37.0	NS	NS
48-h IVDMD	42.9	43.2	41.9	43.9	NS	NS
Observed-Expected DMD	-14.8	-10.2	-11.6	-11.9	NS	NS
Total Ash	5.6	4.6	4.9	4.7	NS	NS
N	1.42	1.88	1.35	1.66	NS	NS
P	.17	.26	.19	.24	0.05	NS
K	.94	1.13	1.03	1.05	NS	NS
Ca	.69	.84	.69	.75	NS	NS
Mg	.26	.21	.24	.26	NS	0.01
Na	.15	.11	.10	.13	NS	NS
	Parts per million					
Cu	6.1	7.5	2.8	7.6	0.001	NS
Mn	1292.6	1451.3	1372.8	1780.2	NS	NS
Fe	193.4	77.5	86.6	62.1	NS	NS
Zn	44.8	38.0	40.4	38.5	NS	NS

[1] Significance is $\propto$ level at which the mean difference between study sites was statistically different than 0 (paired-sample t-test), NS indicates not significant at $\propto_{0.05}$.

Table 9—Results of this study compared with those of others [1]

Study and location	Total ash	N	P	Ca	NDF	ADF	Lignin/ cutin	48-h IVDMD
Klein (1965): [2]								
Woronkofski & Coronation	+1.5	+0.80	+0.08	+0.22				
Islands, southeastern Alaska	(2.2)	(0.56)	(0.07)	(0.40)				
Schoen and Wallmo (1979): [3]								
Admiralty Island,		+0.26			-9.3	-2.2	-0.1	
southeastern Alaska		(0.23)			(6.5)	(5.1)	(4.0)	
Rose (1982): [4]								
Annette Island,		-0.35	-0.03		+2.5	+3.5	+0.9	
southeastern Alaska		(0.58)	(0.10)		(9.4)	(4.8)	(5.7)	
Hanley (1980): [5]		-0.02			-3.9	-4.2	-2.2	
western Washington		(0.62)			(8.2)	(6.2)	(3.0)	
Rochelle (1980): [6]		0			-11.4	-3.8	+3.7	+4.3
Vancouver Island, B.C.		(0.11)			(8.0)	(10.1)	(3.8)	(5.7)

[1] Values are the mean (and standard deviation) difference between this study and others (other study minus this study).
[2] Five comparisons involving *Fauria crista-galli, Carex lyngbyaei, Lysichiton americanum,* and *Vaccinium ovalifolium.*
[3] Eight comparisons involving *Tiarella trifoliata, Rubus pedatus, Cornus canadensis, Coptis aspleniifolia, Tsuga heterophylla, Vaccinium* spp., *Menziesia ferruginea,* and *Usnea* spp.
[4] Twenty comparisons involving *Cornus canadensis, Coptis aspleniifolia, Lysichiton americanum, Maianthemum dilatatum, Rubus pedatus, Streptopus* spp., *Tiarella trifoliata, Vaccinium* spp., and *Usnea* spp.
[5] Fifteen comparisons involving *Tsuga heterophylla, Cornus canadensis, Menziesia ferruginea, Oplopanax horridum, Rubus pedatus, Rubus spectabilis,* and *Maianthemum dilatatum.*
[6] Six comparisons involving *Vaccinium alaskensis* and *Tsuga heterophylla.*

Table 10—Nutrient requirements of beef cattle [1]

	Growing and finishing steers and heifers	Dry pregnant cows	Lactating cows	Mature bulls
	kcal g^{-1}			
Digestible energy	2.2 - 3.1	1.9 - 2.1	1.9 - 2.0	2.0 - 2.3
	Percent			
Crude protein	8.5 - 9.5	5.9 - 8.8	9.2 - 10.9	8.5 - 10.2
Digestible protein	5.0 - 5.6	2.8 - 5.1	5.4 - 6.4	4.8 - 6.3
P	.18 - .70	.18	.18 - .39	.18 - .39
K	.6 - .8	.6 - .8	.6 - .8	.6 - .8
Ca	.18 - 1.04	.18	.18 - .44	.18 - .44
Mg	.04 - .10	.04 - 1.10	.18	.18
Na	.06	.06	.06	.06
	Parts per million			
Cu	4.0	4.0	4.0	4.0
Mn	1.0 - 10.0	20.0	1.0 - 10.0	1.0 - 10.0
Fe	10.0	10.0	10.0	10.0
Zn	20.0 - 30.0	20.0 - 30.0	20.0 - 30.0	20.0 - 30.0

[1] National Research Council. Nutrient requirements of beef cattle. National Academy of Sciences. Washington, D.C. 1976. 56 p.

The National Research Council's requirements for crude protein for beef cattle are based on assumed protein digestibility of 47 to 77 percent, values that are typical for phenolic-free forages. Native forages, especially browses, that are utilized by wildlife, however, may contain appreciable amounts of phenolics or other secondary compounds which reduce protein digestibility. For example, Mould and Robbins (1981) found that fireweed (*Epilobium angustifolium*), which was 12 percent crude protein and 44.2 percent phenolics, had an apparent protein digestibility of 6.1 percent, compared with 68.9 percent digestibility for phenolic-free forages with 12 percent crude protein. The degree to which secondary compounds inhibit digestibility of protein in the Hawk Inlet forages is unknown, but if effects similar to those observed by Mould and Robbins are common, then N availability could be a major nutritional problem for herbivores in southeastern Alaska forests.

Except in forbs and shrub leaves, P concentration was marginal to inadequate in the Hawk Inlet forages. During late summer and fall, it was marginal to inadequate for maintenance and inadequate for lactation in all forage classes. Ca:P ratios were higher than unity (average about 3.3:1, table 5) but not excessively high. High ratios of Ca to P (10:1) reduce the availability of P below what its concentration alone would indicate. Excess Mg may form insoluble P complexes, and excess Mn may form insoluble complexes with Ca (Robbins 1983). Ca levels in the Hawk Inlet forages were more than adequate the year around—about 2 to 8 times minimum requirements. Mg and Mn also were excessive—about 2 to 5 times the minimum requirement for Mg and 12 to 400 times the minimum requirement for Mn.

K levels were marginal to inadequate in conifers the year around and in shrub stems and graminoids during winter. Forbs, half-shrubs, shrub leaves, and algae were more than adequate year around sources. Rockweed alga may be an important source of K during prolonged winter conditions when forbs and half-shrubs are buried with snow. Similarly, forbs would be the major source of Na year around, except when buried with snow. Rockweed alga and graminoids growing along the beach were very high in Na.

Cu concentrations were generally above minimum requirements in all forage classes throughout the year except for conifers and graminoids during winter. Shrubs are potentially the most important source of Cu throughout the year.

Fe concentrations were generally well above minimum requirements in most forages throughout the year. Fe concentrations were especially high in moss, rockweed alga, and graminoids.

Zn levels were above minimum requirements in forbs year around and in shrubs during summer. They were marginal in other forage classes throughout the year and below minimum requirements in conifers in spring and graminoids in fall.

Generally, the Hawk Inlet forages, which did not differ markedly from forages collected elsewhere in southeastern Alaska, appeared to be most limited in digestible energy, P, and probably N. Forbs, half-shrubs, and shrub leaves were consistently the most nutritious forages. Rockweed alga, a common intertidal plant, is a potentially important source of K and Fe when these elements are in short supply in the forest. Nutritional deficiencies are likely to be greatest during winter, especially during periods of snow accumulation, when the availability of forage is restricted and the metabolic costs of locomotion are elevated. During winter, evergreen forbs and half-shrubs are far superior nutritionally to any other forages.

The importance of plant nutrients in limiting herbivore populations varies with specific dietary requirements of species, efficiency of utilizing forage, forage availability, diet choice, and energy requirements. Our identification of digestible energy, N and P as potentially important factors limiting herbivore populations is applicable in a very general sense only.

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Appendix — Results of Chemical Analyses of Hawk Inlet Forages

Neutral Detergent Fiber

Forage class and species	Jan. 9	Mar. 20	May 27	Aug. 3	Sept. 29	Nov. 30
	Percent					
Forbs and ferns:						
Coptis aspleniifolia	43.2	42.3	48.7	45.7	42.6	40.1
Dryopteris dilatata	52.0	67.3	48.5	42.1	46.2	42.0
Listera cordata			21.9	25.8		
Lysichiton americanum		15.6	17.8	22.3	27.6	
Maianthemum dilatatum			24.6	26.0		
Moneses uniflora	29.2	29.3	29.9	27.1	27.0	28.9
Streptopus spp.			24.7	29.8		
Tiarella trifoliata	37.0	34.9	31.5	34.0	34.0	35.1
Half-shrubs:						
Cornus canadensis	35.6	36.6	22.8	40.3	30.6	27.9
Rubus pedatus	35.9	34.7	33.7	33.9	32.8	34.3
Vaccinium spp.[1]	55.4	56.4	52.2	55.8	51.9	48.2
Shrubs:						
Menziesia ferruginea—						
Leaves			39.4	33.4	41.7	
Stems	71.9	77.2		79.0	73.8	72.3
Oplopanax horridum—						
Leaves			37.5	30.0	25.5	
Stems			43.7	51.0	60.4	71.9
Rubus spectabilis—						
Leaves			27.0	31.4	32.9	
Stems			53.3	75.2	70.0	
Vaccinium alaskensis—						
Leaves			51.2	55.6	53.2	
Stems	66.6	70.6	56.4	70.3	71.3	64.2
Conifers:						
Picea sitchensis	61.5	58.7	61.2	60.6	57.9	57.1
Tsuga heterophylla	64.3	52.3	48.6	48.5	52.1	48.3
Graminoids:						
Deschampsia caespitosa	70.7		54.9	56.5	78.2	85.3
Carex lyngbyaei			59.2	64.5	68.9	77.6
Lichens:						
Usnea spp.	33.0	21.5	30.2	25.6	33.8	20.8
Moss:						
Rhytidiadelphus loreus	86.3	82.5	80.4	77.7	80.9	82.7
Algae:						
Fucus furcatus	35.7	25.7	26.1	18.3	37.0	24.1

[1] Decumbent, evergreen variety.

Acid Detergent Fiber (sequential)

Forage class and species	Jan. 9	Mar. 20	May 27	Aug. 3	Sept. 29	Nov. 30
	Percent					
Forbs and ferns:						
Coptis aspleniifolia	30.4	27.7	30.1	29.8	27.7	26.3
Dryopteris dilatata	37.5	55.6	29.0	33.3	35.8	26.2
Listera cordata			15.9	17.2		
Lysichiton americanum		7.3	11.5	12.8	18.2	18.1
Maianthemum dilatatum			16.9	15.8		
Moneses uniflora	20.2	18.1	14.0	17.2	17.3	
Streptopus spp.			16.9	21.6		
Tiarella trifoliata	27.8	25.9	26.4	24.0	27.6	20.1
Half-shrubs:						
Cornus canadensis	21.7	20.6	18.9	26.6	19.6	21.3
Rubus pedatus	19.1	15.5	17.2	17.6	17.6	17.6
Vaccinium spp.[1]	39.5	34.1	32.7	39.1	35.1	31.8
Shrubs:						
Menziesia ferruginea—						
Leaves			21.5	19.7	27.8	
Stems	50.5	53.6		54.7	49.3	72.3
Oplopanax horridum—						
Leaves			16.2	16.8	17.2	
Stems			30.9	37.3	44.3	53.7
Rubus spectabilis—						
Leaves			11.7	15.2	15.2	
Stems			34.3	49.1	43.6	
Vaccinium alaskensis—						
Leaves			27.9	32.6	31.2	
Stems	50.3	51.6	41.8	53.3	53.1	45.2
Conifers:						
Picea sitchensis	46.1	44.3	44.8	47.1	43.4	40.6
Tsuga heterophylla	51.0	38.5	33.6	36.0	39.2	33.9
Graminoids:						
Deschampsia caespitosa	37.3		28.0	25.2	42.9	48.4
Carex lyngbyaei			26.6	36.8	34.3	41.3
Lichens:						
Usnea spp.	5.8	5.2	4.8	3.6	3.4	4.0
Moss:						
Rhytidiadelphus loreus	58.6	51.1	48.7	53.0	48.4	50.0
Algae:						
Fucus furcatus	29.7	17.9	18.8	12.4	18.5	16.0

[1] Decumbent, evergreen variety.

Cellulose

Forage class and species	Jan. 9	Mar. 20	May 27	Aug. 3	Sept. 29	Nov. 30
			Percent			
Forbs and ferns:						
Coptis aspleniifolia	25.6	22.4	25.4	24.4	25.3	21.2
Dryopteris dilatata	19.6	26.2	20.0	17.3	24.3	15.1
Listera cordata			10.0	16.8		
Lysichiton americanum		5.3	9.5	11.4	15.5	
Maianthemum dilatatum			15.4	12.8		
Moneses uniflora	15.0	12.2	10.7	11.9	15.6	14.0
Streptopus spp.			15.6	18.6		
Tiarella trifoliata	18.1	15.0	10.5	15.6	17.8	14.2
Half-shrubs:						
Cornus canadensis	19.0	16.6	7.7	15.8	18.0	11.9
Rubus pedatus	16.0	12.4	14.1	14.4	13.8	13.6
Vaccinium spp.[1]	29.7	19.4	17.9	23.7	23.5	20.3
Shrubs:						
Menziesia ferruginea—						
Leaves			14.8	13.7	16.4	
Stems	31.6	33.6		33.0	31.7	28.1
Oplopanax horridum—						
Leaves			9.4	13.9	12.0	
Stems			20.6	28.0	31.7	37.8
Rubus spectabilis—						
Leaves			8.7	9.2	9.1	
Stems			25.2	32.3	31.9	
Vaccinium alaskensis—						
Leaves			13.9	15.9	16.4	
Stems	29.8	29.6	22.2	31.8	33.0	28.2
Conifers:						
Picea sitchensis	26.7	23.3	26.7	29.3	26.8	27.1
Tsuga heterophylla	32.7	18.1	18.2	20.6	24.2	20.4
Graminoids:						
Deschampsia caespitosa	22.1		23.1	21.3	33.6	37.4
Carex lyngbyaei			22.1	31.0	24.8	30.4
Lichens:						
Usnea spp.	2.5	2.5	2.2	2.0	0.1	0.5
Moss:						
Rhytidiadelphus loreus	35.3	29.0	29.4	31.6	30.2	29.4
Algae:						
Fucus furcatus	13.2	5.9	6.4	5.1	5.3	4.9

[1] Decumbent, evergreen variety.

Lignin/cutin

Forage class and species	Jan. 9	Mar. 20	May 27	Aug. 3	Sept. 29	Nov. 30
	Percent					
Forbs and ferns:						
Coptis aspleniifolia	4.8	4.6	4.7	5.4	2.3	3.6
Dryopteris dilatata	17.8	28.3	9.0	16.0	11.6	9.7
Listera cordata			6.0	0.4		
Lysichiton americanum		2.0	2.0	1.4	2.7	
Maianthemum dilatatum			1.5	1.4		
Moneses uniflora	3.7	5.4	3.3	5.4	4.6	3.8
Streptopus spp.			1.3	0.5		
Tiarella trifoliata	9.4	10.7	15.9	8.4	9.8	3.9
Half-shrubs:						
Cornus canadensis	1.6	3.1	11.2	10.8	1.4	8.7
Rubus pedatus	3.0	2.8	3.1	3.2	2.9	1.5
Vaccinium spp.[1]	9.8	14.8	14.8	15.3	11.6	10.3
Shrubs:						
Menziesia ferruginea—						
Leaves			6.7	6.0	10.8	
Stems	18.9	19.9		20.8	15.7	15.8
Oplopanax horridum—						
Leaves			6.8	2.9	3.8	
Stems			10.2	9.2	10.5	15.9
Rubus spectabilis—						
Leaves			3.0	6.0	6.2	
Stems			9.1	16.7	11.4	
Vaccinium alaskensis—						
Leaves			14.0	16.7	14.8	
Stems	20.5	16.7	19.6	19.4	17.0	15.4
Conifers:						
Picea sitchensis	19.4	21.1	18.1	17.8	16.1	12.1
Tsuga heterophylla	12.2	20.4	15.4	15.5	14.8	12.4
Graminoids:						
Deschampsia caespitosa	4.4		4.9	3.9	8.2	9.4
Carex lyngbyaei			4.5	5.8	8.4	10.1
Lichens:						
Usnea spp.	2.1	1.4	2.7	1.6	3.3	2.2
Moss:						
Rhytidiadelphus loreus	21.0	21.5	19.3	21.3	17.4	19.8
Algae:						
Fucus furcatus	16.4	12.0	12.4	7.2	12.1	11.1

[1] Decumbent, evergreen variety.

In-Vitro Dry-Matter Digestibility

Forage class and species	Jan. 9 12 h	Jan. 9 48 h	Mar. 20 12 h	Mar. 20 48 h	May 27 12 h	May 27 48 h	Aug. 3 12 h	Aug. 3 48 h	Sept. 29 12 h	Sept. 29 48 h	Nov. 30 12 h	Nov. 30 48 h
	Percent											
Forbs and ferns:												
Coptis aspleniifolia	46.9	72.4	50.2	71.2	47.2	61.4	44.0	63.6	44.9	62.7	46.7	70.7
Dryopteris dilatata	35.4	48.2	21.1	21.4	42.3	60.5	24.8	25.1	32.3	48.5	42.3	56.4
Listera cordata					64.7	79.3	57.7	72.7				
Lysichiton americanum			80.6	86.6	61.7	77.0	53.6	75.5	58.0	72.9		
Maianthemum dilatatum					60.8	65.5	66.6	77.4				
Moneses uniflora	54.8	62.2	53.9	70.0	51.1	74.0	50.9	66.1	56.4	69.5	57.1	68.0
Streptopus spp.					60.7	70.1	51.0	69.8				
Tiarella trifoliata	44.1	61.3	44.8	61.6	45.8	54.1	38.8	43.5	42.8	51.7	42.7	54.6
Half-shrubs:												
Cornus canadensis	46.4	75.6	46.5	73.1	51.9	57.3	41.0	58.4	47.2	62.5	49.4	68.7
Rubus pedatus	38.0	54.3	42.2	48.1	39.7	39.5	39.8	46.3	39.6	50.2	43.8	66.8
Vaccinium spp.[1]	37.9	48.4	40.6	48.7	38.9	54.7	31.9	42.4	39.5	53.8	43.5	54.9
Shrubs:												
Menziesia ferruginea—												
Leaves					45.9	62.8	39.3	46.6	34.4	41.6		
Stems	21.2	27.1	16.7	19.0			14.4	21.2	18.4	21.2	21.5	31.3
Oplopanax horridum—												
Leaves					67.0	73.6	55.6	74.0	57.4	72.4		
Stems					62.7	80.1	45.6	56.0	40.4	52.2	24.5	26.5
Rubus spectabilis—												
Leaves					48.2	59.3	47.7	43.3	39.8	35.7		
Stems					34.6	49.7	17.7	24.9	24.0	26.5		
Vaccinium alaskensis—												
Leaves					44.3	51.8	37.0	45.8	40.7	42.4		
Stems	28.0	36.1	24.2	27.8	41.8	49.6	21.2	27.8	23.5	27.1	26.7	36.2
Conifers:												
Picea sitchensis	29.8	30.1	29.1	29.7	24.8	28.3	25.2	28.7	28.7	26.7	28.6	29.7
Tsuga heterophylla	25.5	26.2	31.9	29.8	27.2	33.3	28.8	31.0	31.3	28.9	32.9	33.5
Graminoids:												
Deschampsia caespitosa	29.7	44.6			44.9	43.3	40.7	63.3	22.6	20.1	10.8	18.2
Carex lyngbyaei					50.5	64.3	32.5	42.0	27.7	27.3	13.1	23.9
Lichens:												
Usnea spp.	17.1	20.7	19.3	17.2	19.0	17.0	19.0	15.2	21.6	22.5	16.7	17.1
Moss:												
Rhytidiadelphus loreus	11.2	12.4	13.6	14.5	17.9	15.0	17.8	20.8	16.2	14.1	16.3	18.9
Algae:												
Fucus furcatus	37.9	37.1	42.7	48.4	41.9	33.4	52.9	30.8	47.5	30.2	50.2	37.9

[1] Decumbent, evergreen variety.

Nitrogen

Forage class and species	Jan. 9	Mar. 20	May 27	Aug. 3	Sept. 29	Nov. 30
	Percent					
Forbs and ferns:						
Coptis aspleniifolia	1.37	1.50	2.98	1.69	1.73	1.56
Dryopteris dilatata	1.92	1.80	3.63	1.82	1.93	2.14
Listera cordata			2.80	2.22		
Lysichiton americanum		8.00	5.61	5.14	3.78	
Maianthemum dilatatum			2.61	1.45		
Moneses uniflora	2.29	2.46	1.83	1.72	1.97	1.81
Streptopus spp.			4.56	2.39		
Tiarella trifoliata	1.54	1.80	3.27	1.98	1.78	1.86
Half-shrubs:						
Cornus canadensis	1.70	1.58	3.30	2.11	1.66	1.68
Rubus pedatus	1.65	1.92	3.00	1.77	2.04	1.77
Vaccinium spp.[1]	1.50	1.48	1.95	1.20	1.44	1.53
Shrubs:						
Menziesia ferruginea—						
Leaves			3.51	2.00	1.94	
Stems	1.12	.97	2.52	.72	.80	.96
Oplopanax horridum—						
Leaves			5.20	2.69	2.04	
Stems			5.08	.60	.51	1.90
Rubus spectabilis—						
Leaves			2.94	2.04	1.77	
Stems			1.30	.70	.89	
Vaccinium alaskensis—						
Leaves			3.69	2.53	2.14	
Stems	1.50	1.54	2.16	1.10	1.05	1.15
Conifers:						
Picea sitchensis	.95	1.20	1.04	1.05	.89	1.15
Tsuga heterophylla	.84	1.16	.94	1.12	.99	1.03
Graminoids:						
Deschampsia caespitosa	1.14		3.55	1.26	.50	.69
Carex lyngbyaei			2.10	.67	1.02	.86
Lichens:						
Usnea spp.	0.42	0.50	0.36	0.53	0.45	0.35
Moss:						
Rhytidiadelphus loreus	.60	.64	.57	.71	.57	.62
Algae:						
Fucus furcatus	1.23	1.90	1.74	.99	1.23	1.35

[1] Decumbent, evergreen variety.

Phosphorus

Forage class and species	Jan. 9	Mar. 20	May 27	Aug. 3	Sept. 29	Nov. 30
	Percent					
Forbs and ferns:						
Coptis aspleniifolia	0.17	0.17	0.40	0.19	0.19	0.19
Dryopteris dilatata	.28	.24	.49	.15	.12	.41
Listera cordata			.48	.36		
Lysichiton americanum		.98	.62	.26	.22	
Maianthemum dilatatum			.38	.21		
Moneses uniflora	.29	.33	.27	.20	.24	.27
Streptopus spp.			.54	.21		
Tiarella trifoliata	.20	.22	.47	.17	.18	.23
Half-shrubs:						
Cornus canadensis	.18	.19	.47	.17	.15	.18
Rubus pedatus	.21	.24	.37	.18	.21	.22
Vaccinium spp.[1]	.15	.17	.19	.12	.16	.17
Shrubs:						
Menziesia ferruginea—						
Leaves			.36	.14	.23	
Stems	.12	.14	.29	.11	.11	.13
Oplopanax horridum—						
Leaves			.91	.22	.17	
Stems			.92	.11	.09	.22
Rubus spectabilis—						
Leaves			.41	.29	.35	
Stems			.37	.11	.12	
Vaccinium alaskensis—						
Leaves			.32	.14	.15	
Stems	.18	.22	.28	.13	.14	.14
Conifers:						
Picea sitchensis	.19	.24	.14	.18	.16	.22
Tsuga heterophylla	.15	.28	.15	.19	.21	.18
Graminoids:						
Deschampsia caespitosa	.14		.29	.16	.06	.06
Carex lyngbyaei			.33	.11	.12	.11
Lichens:						
Usnea spp.	0.08	0.14	0.07	0.12	0.07	0.10
Moss:						
Rhytidiadelphus loreus	.12	.14	.12	.14	.14	.14
Algae:						
Fucus furcatus	.16	.24	.17	.10	.16	.16

[1] Decumbent, evergreen variety.

Potassium

Forage class and species	Jan. 9	Mar. 20	May 27	Aug. 3	Sept. 29	Nov. 30
	Percent					
Forbs and ferns:						
Coptis aspleniifolia	1.47	1.44	2.17	1.81	1.62	1.39
Dryopteris dilatata	1.96	1.44	3.95	2.28	2.62	2.30
Listera cordata			3.55	4.43		
Lysichiton americanum		3.73	2.50	1.97	1.75	
Maianthemum dilatatum			2.11	2.68		
Moneses uniflora	1.59	1.67	1.20	1.47	1.54	3.30
Streptopus spp.			5.00	3.64		
Tiarella trifoliata	2.46	2.19	3.16	2.24	2.49	2.55
Half-shrubs:						
Cornus canadensis	1.08	1.00	1.52	1.03	.76	.84
Rubus pedatus	1.45	1.39	1.76	1.25	1.23	1.11
Vaccinium spp.[1]	.78	.74	.89	.56	.78	.72
Shrubs:						
Menziesia ferruginea—						
Leaves			1.60	.81	1.16	
Stems	.33	.37	3.19	.58	.30	.30
Oplopanax horridum—						
Leaves			3.34	1.72	2.23	
Stems			6.30	.43	1.63	.53
Rubus spectabilis—						
Leaves			1.35	1.37	1.17	
Stems			2.83	.53	.54	
Vaccinium alaskensis—						
Leaves			1.14	.56	1.54	
Stems	1.07	.62	1.48	.25	.52	.46
Conifers:						
Picea sitchensis	.64	.62	.54	.68	.56	.90
Tsuga heterophylla	.47	.57	.43	.54	.46	.57
Graminoids:						
Deschampsia caespitosa	.60		2.27	1.76	.44	.24
Carex lyngbyaei			2.56	.77	1.92	.14
Lichens:						
Usnea spp.	0.23	0.29	0.12	0.26	0.21	0.19
Moss:						
Rhytidiadelphus loreus	.47	.50	.36	.45	.42	.40
Algae:						
Fucus furcatus	2.18	2.80	2.59	2.44	2.39	3.70

[1] Decumbent, evergreen variety.

Calcium

Forage class and species	Jan. 9	Mar. 20	May 27	Aug. 3	Sept. 29	Nov. 30
	Percent					
Forbs and ferns:						
Coptis aspleniifolia	0.90	0.85	0.37	0.80	0.98	0.82
Dryopteris dilatata	.45	.70	.36	.59	1.05	.47
Listera cordata			.42	.83		
Lysichiton americanum		1.47	.64	1.42	1.77	
Maianthemum dilatatum			.46	.54		
Moneses uniflora	.56	.51	.46	.50	.63	1.30
Streptopus spp.			.64	1.65		
Tiarella trifoliata	1.54	2.58	1.25	1.90	2.25	2.19
Half-shrubs:						
Cornus canadensis	2.94	2.38	1.40	2.97	3.11	2.70
Rubus pedatus	.71	.85	.38	.77	.97	.62
Vaccinium spp.[1]	.77	.82	.88	.76	.88	.97
Shrubs:						
Menziesia ferruginea—						
Leaves			.51	.60	.75	
Stems	.34	.25	.86	.19	.23	.23
Oplopanax horridum—						
Leaves			.14	1.42	2.31	
Stems			.28	.75	1.31	1.18
Rubus spectabilis—						
Leaves			.69	.77	1.22	
Stems			.68	.21	.49	
Vaccinium alaskensis—						
Leaves			.72	1.33	1.60	
Stems	.68	.61	.60	.59	.64	.76
Conifers:						
Picea sitchensis	.24	.32	.39	.45	.42	.35
Tsuga heterophylla	.25	.31	.34	.37	.36	.39
Graminoids:						
Deschampsia caespitosa	.19		.16	.48	.09	.11
Carex lyngbyaei			.16	.07	.66	.55
Lichens:						
Usnea spp.	0.15	0.24	0.41	0.31	0.24	0.36
Moss:						
Rhytidiadelphus loreus	.28	.27	.27	.36	.28	.36
Algae:						
Fucus furcatus	.92	.94	.85	1.94	.77	.94

[1] Decumbent, evergreen variety.

Magnesium

Forage class and species	Jan. 9	Mar. 20	May 27	Aug. 3	Sept. 29	Nov. 30
	Percent					
Forbs and ferns:						
Coptis aspleniifolia	0.33	0.31	0.20	0.35	0.31	0.35
Dryopteris dilatata	.40	.26	.30	.61	.45	.46
Listera cordata			.16	.26		
Lysichiton americanum		.22	.21	.25	.25	
Maianthemum dilatatum			.20	.23		
Moneses uniflora	.18	.19	.18	.18	.21	.41
Streptopus spp.			.23	.42		
Tiarella trifoliata	.60	.37	.31	.37	.38	.35
Half-shrubs:						
Cornus canadensis	.53	.43	.37	.61	.52	.45
Rubus pedatus	.61	.53	.36	.48	.48	.40
Vaccinium spp.[1]	.18	.18	.24	.18	.20	.20
Shrubs:						
Menziesia ferruginea—						
Leaves			.38	.42	.41	
Stems	.17	.08	.47	.11	.09	.08
Oplopanax horridum—						
Leaves			.23	.19	.15	
Stems			.23	.14	.20	.16
Rubus spectabilis—						
Leaves			.40	.38	.42	
Stems			.25	.10	.15	
Vaccinium alaskensis—						
Leaves			.33	.45	.38	
Stems	.18	.14	.22	.16	.13	.15
Conifers:						
Picea sitchensis	.07	.08	.08	.08	.08	.09
Tsuga heterophylla	.09	.10	.09	.09	.09	.12
Graminoids:						
Deschampsia caespitosa	.36		.10	.15	.12	.12
Carex lyngbyaei			.15	.09	.17	.14
Lichens:						
Usnea spp.	0.05	0.07	0.06	0.07	0.08	0.05
Moss:						
Rhytidiadelphus loreus	.06	.11	.10	.10	.09	.09
Algae:						
Fucus furcatus	.71	.74	.72	.81	.54	.79

[1] Decumbent, evergreen variety.

Sodium

Forage class and species	Jan. 9	Mar. 20	May 27	Aug. 3	Sept. 29	Nov. 30
	Percent					
Forbs and ferns:						
Coptis aspleniifolia	0.09	0.05	0.06	0.06	0.05	0.05
Dryopteris dilatata	.22	.05	.04	.17	.11	.24
Listera cordata			.18	.35		
Lysichiton americanum		.58	.46	1.67	1.31	
Maianthemum dilatatum			.72	.59		
Moneses uniflora	.10	.16	.07	.09	.08	.27
Streptopus spp.			.04	.08		
Tiarella trifoliata	.35	.20	.12	.12	.13	.20
Half-shrubs:						
Cornus canadensis	.07	.04	.09	.06	.02	.03
Rubus pedatus	.03	.11	.04	.07	.07	.12
Vaccinium spp.[1]	.08	.07	.13	.09	.09	.08
Shrubs:						
Menziesia ferruginea—						
Leaves			.09	.52	.80	
Stems	.11	.04	.18	.12	.06	.05
Oplopanax horridum—						
Leaves			.08	.78	.67	
Stems			.20	.25	.51	.12
Rubus spectabilis—						
Leaves			.12	.22	.30	
Stems			.21	.15	.15	
Vaccinium alaskensis—						
Leaves			.18	.41	.31	
Stems	.07	.04	.11	.10	.02	.06
Conifers:						
Picea sitchensis	.06	.06	.04	.08	.11	.05
Tsuga heterophylla	.07	.06	.09	.07	.06	.12
Graminoids:						
Deschampsia caespitosa	1.79		.30	.27	.75	.28
Carex lyngbyaei			.16	1.12	.07	.07
Lichens:						
Usnea spp.	0.13	0.04	0.07	0.07	0.07	0.04
Moss:						
Rhytidiadelphus loreus	.09	.12	.06	.03	.06	.07
Algae:						
Fucus furcatus	2.96	3.68	1.19	3.58	1.83	3.72

[1] Decumbent, evergreen variety.

Copper

Forage class and species	Jan. 9	Mar. 20	May 27	Aug. 3	Sept. 29	Nov. 30
	Parts per million					
Forbs and ferns:						
Coptis aspleniifolia	6	2	10	2	10	2
Dryopteris dilatata	9	18	20	< 1	6	2
Listera cordata			14	8		
Lysichiton americanum		18	23	5	9	
Maianthemum dilatatum			6	< 1		
Moneses uniflora	10	7	9	3	9	11
Streptopus spp.			16	4		
Tiarella trifoliata	8	3	15	5	5	3
Half-shrubs:						
Cornus canadensis	6	2	12	4	3	4
Rubus pedatus	7	5	14	5	6	6
Vaccinium spp.[1]	7	7	12	4	8	4
Shrubs:						
Menziesia ferruginea—						
Leaves			17	3	10	
Stems	8	10	24	7	13	9
Oplopanax horridum—						
Leaves			25	17	6	
Stems			20	7	5	15
Rubus spectabilis—						
Leaves			6	6	3	
Stems			10	42	3	
Vaccinium alaskensis—						
Leaves			16	12	6	
Stems	11	13	17	15	8	8
Conifers:						
Picea sitchensis	2	7	< 1	6	2	2
Tsuga heterophylla	5	4	1	7	2	2
Graminoids:						
Deschampsia caespitosa	8		4	8	< 1	< 1
Carex lyngbyaei			5	4	1	1
Lichens:						
Usnea spp.	< 1	4	< 1	6	< 1	< 1
Moss:						
Rhytidiadelphus loreus	7	5	5	8	3	3
Algae:						
Fucus furcatus	1	5	< 1	5	< 1	< 1

[1] Decumbent, evergreen variety.

Manganese

Forage class and species	Jan. 9	Mar. 20	May 27	Aug. 3	Sept. 29	Nov. 30
			Parts per million			
Forbs and ferns:						
Coptis aspleniifolia	310.2	327.5	131.8	306.9	357.7	521.8
Dryopteris dilatata	1,205.4	350.4	72.6	297.9	408.3	1,674.0
Listera cordata			744.9	1,081.0		
Lysichiton americanum		1,063.0	953.0	364.0	4,799.0	
Maianthemum dilatatum			261.9	785.8		
Moneses uniflora	594.6	736.7	494.8	490.2	625.1	717.5
Streptopus spp.			143.8	448.4		
Tiarella trifoliata	567.9	331.4	127.9	178.0	241.7	484.4
Half-shrubs:						
Cornus canadensis	212.1	233.2	144.0	197.2	213.3	269.9
Rubus pedatus	981.4	1,366.0	763.3	1,082.0	1,507.0	1,726.0
Vaccinium spp.[1]	3,038.0	3,868.0	2,576.0	2,877.0	3,134.0	3,211.0
Shrubs:						
Menziesia ferruginea—						
Leaves			19,620.0	16,370.0	13,980.0	
Stems	4,127.0	6,096.0	19,997.3	3,111.0	4,125.0	5,379.0
Oplopanax horridum—						
Leaves			162.8	281.4	283.1	
Stems			75.8	80.1	97.2	259.1
Rubus spectabilis—						
Leaves			124.9	57.4	72.2	
Stems			39.3	31.9	39.6	
Vaccinium alaskensis—						
Leaves			1,886.0	3,125.0	872.8	
Stems	1,752.0	1,493.0	3,274.0	2,818.0	601.7	2,191.0
Conifers:						
Picea sitchensis	1,577.0	1,666.0	848.2	843.7	1,221.0	1,640.0
Tsuga heterophylla	2,064.0	2,758.0	1,564.0	1,457.0	2,748.0	1,092.0
Graminoids:						
Deschampsia caespitosa	286.1		106.3	559.3	31.8	21.8
Carex lyngbyaei			316.2	39.1	1,095.0	1,332.0
Lichens:						
Usnea spp.	221.1	385.1	133.7	186.1	158.6	240.7
Moss:						
Rhytidiadelphus loreus	1,086.1	943.0	1,336.0	1,261.0	808.1	870.6
Algae:						
Fucus furcatus	24.9	35.6	67.7	31.9	53.3	47.4

[1] Decumbent, evergreen variety.

Iron

Forage class and species	Jan. 9	Mar. 20	May 27	Aug. 3	Sept. 29	Nov. 30
	Parts per million					
Forbs and ferns:						
Coptis aspleniifolia	136	39	55	30	39	77
Dryopteris dilatata	187	160	81	28	73	105
Listera cordata			87	82		
Lysichiton americanum		88	104	88	127	
Maianthemum dilatatum			43	36		
Moneses uniflora	637	81	54	42	67	133
Streptopus spp.			76	60		
Tiarella trifoliata	510	67	97	287	108	358
Half-shrubs:						
Cornus canadensis	126	54	55	55	45	117
Rubus pedatus	161	160	50	44	59	119
Vaccinium spp.[1]	103	49	51	27	55	60
Shrubs:						
Menziesia ferruginea—						
Leaves			76	42	68	
Stems	29	17	58	4	21	8
Oplopanax horridum—						
Leaves			82	67	43	
Stems			40	12	14	87
Rubus spectabilis—						
Leaves			41	49	86	
Stems			21	18	19	
Vaccinium alaskensis—						
Leaves			53	58	43	
Stems	17	31	40	23	18	10
Conifers:						
Picea sitchensis	9	20	17	22	45	27
Tsuga heterophylla	115	29	59	72	68	54
Graminoids:						
Deschampsia caespitosa	990		21	110	50	100
Carex lyngbyaei			30	110	42	225
Lichens:						
Usnea spp.	77	51	42	63	60	47
Moss:						
Rhytidiadelphus loreus	434	241	338	371	337	369
Algae:						
Fucus furcatus	120	155	183	153	138	200

[1] Decumbent, evergreen variety.

Zinc

Forage class and species	Jan. 9	Mar. 20	May 27	Aug. 3	Sept. 29	Nov. 30
	Parts per million					
Forbs and ferns:						
Coptis aspleniifolia	187.3	161.2	118.0	148.0	191.3	260.0
Dryopteris dilatata	84.1	38.7	33.8	10.3	27.8	70.3
Listera cordata			59.6	77.6		
Lysichiton americanum		68.3	45.8	26.6	33.0	
Maianthemum dilatatum			27.2	19.9		
Moneses uniflora	34.4	41.2	32.6	28.2	34.5	38.3
Streptopus spp.			60.1	44.7		
Tiarella trifoliata	80.5	45.2	40.2	35.8	44.1	34.6
Half-shrubs:						
Cornus canadensis	23.1	18.2	33.9	24.6	20.1	16.1
Rubus pedatus	29.3	27.2	36.5	22.4	34.1	42.1
Vaccinium spp.[1]	30.8	30.2	38.0	28.5	34.0	38.6
Shrubs:						
Menziesia ferruginea—						
Leaves			89.2	72.4	98.3	
Stems	32.8	17.6	94.1	25.8	46.9	26.0
Oplopanax horridum—						
Leaves			69.2	32.4	26.2	
Stems			50.8	69.1	98.4	43.2
Rubus spectabilis—						
Leaves			58.2	79.7	108.1	
Stems			134.5	88.0	126.8	
Vaccinium alaskensis—						
Leaves			21.6	17.9	16.4	
Stems	39.2	24.6	60.6	47.7	34.2	30.6
Conifers:						
Picea sitchensis	24.9	15.0	23.0	39.0	34.2	30.5
Tsuga heterophylla	22.9	6.2	11.6	18.3	14.8	11.2
Graminoids:						
Deschampsia caespitosa	34.8		16.5	22.9	12.1	16.5
Carex lyngbyaei			29.7	10.9	21.8	28.1
Lichens:						
Usnea spp.	30.1	21.2	21.3	44.0	25.9	29.2
Moss:						
Rhytidiadelphus loreus	23.0	17.6	16.7	34.1	25.9	25.4
Algae:						
Fucus furcatus	24.7	18.6	19.1	16.2	35.3	19.3

[1] Decumbent, evergreen variety.

Total Ash

Forage class and species	Jan. 9	Mar. 20	May 27	Aug. 3	Sept. 29	Nov. 30
	Percent					
Forbs and ferns:						
Coptis aspleniifolia	5.9	5.2		6.3	6.5	6.3
Dryopteris dilatata	7.1	6.1	10.0	4.4	10.9	8.1
Listera cordata						
Lysichiton americanum		10.0	8.3	11.2	11.7	
Maianthemum dilatatum			7.5	8.1		
Moneses uniflora	6.5	4.8	4.3	4.6	5.4	5.4
Streptopus spp.				11.5		
Tiarella trifoliata	11.6	11.0	9.5	11.0	11.7	11.9
Half-shrubs:						
Cornus canadensis	10.9	9.5	7.6	10.7	11.2	10.4
Rubus pedatus	5.8	5.4	5.1	5.5	6.2	5.3
Vaccinium spp.[1]	4.7	4.0	4.7	4.4	4.9	4.9
Shrubs:						
Menziesia ferruginea—						
Leaves			8.7	7.6	8.5	
Stems	2.2	2.1		2.4	1.8	2.0
Oplopanax horridum—						
Leaves			7.9	9.7	12.2	
Stems			11.9	3.0	6.9	4.4
Rubus spectabilis—						
Leaves			5.0	6.0	6.5	
Stems				2.0	2.6	
Vaccinium alaskensis—						
Leaves			4.7	7.6	8.9	
Stems	3.3	3.2		2.8	2.9	3.2
Conifers:						
Picea sitchensis	2.4	2.0	2.4	2.8	3.0	2.8
Tsuga heterophylla	2.2	2.4	2.1	2.4	2.9	2.7
Graminoids:						
Deschampsia caespitosa	14.3		5.0	6.0	4.8	3.4
Carex lyngbyaei			5.8	4.4	6.7	2.9
Lichens:						
Usnea spp.	1.0	1.2	1.4	1.1	1.4	1.4
Moss:						
Rhytidiadelphus loreus	2.4	2.2	2.2	2.0	2.9	2.6
Algae:						
Fucus furcatus	21.1	24.0	13.3	23.0	16.0	25.0

[1] Decumbent, evergreen variety.

HANLEY, THOMAS A.; McKENDRICK, JAY D. Seasonal changes in chemical composition and nutritive value of native forages in a spruce-hemlock forest, southeastern Alaska. Res. Pap. PNW-312. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; **1983.** 41 p.

Twenty-two forages from Admiralty Island, southeastern Alaska, were monitored bimonthly for one year to assess seasonal changes in their chemical composition: neutral detergent fiber, acid detergent fiber, cellulose, lignin/cutin, in-vitro dry-matter digestibility, total nitrogen, phosphorus, potassium, calcium, magnesium, sodium, copper, manganese, iron, and zinc. Seasonal fluctuations were pronounced but generally paralleled the pulse of plant growth in spring-summer. Only minor differences were found in chemical composition of forages from two study areas and results of this study did not differ greatly from results of other studies in southeastern Alaska and the Pacific Northwest. Forbs, half-shrubs, and shrub leaves were consistently the most nutritious forages, especially during winter. Seasonally low levels of digestible energy, nitrogen, and phosphorus were identified as the most important potential limitations of these forages in meeting the nutritional needs of herbivores.

Keywords: Forage production, nutrient analysis, native plants, phytochemistry, phenology, seasonal variations, Alaska (southeastern), southeastern Alaska, wildlife habitat.

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